ENVIRONMENTAL DRIVERS OF DEER POPULATION DYNAMICS AND SPATIAL SELECTION IN SOUTHEAST ALASKA

By

Sophie L. Gilbert

RECOMMENDED:

Dr. David Person

Dr. Mark Lindberg

Dr. Mark Boyce

Dr. Kris Hundertmark
Advisory Committee Chair

Dr. Diane Wagner
Chair, Department of Biology and Wildlife

APPROVED:

Dr. Paul Layer
Dean, Natural Science and Mathematics

Dr. John Eichelberger
Dean of the Graduate School

28 July 2015
Date

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A

DISSERTATION

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By

Sophie L. Gilbert, B.Sc.

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ABSTRACT

The coastal temperate rainforest is one of the rarest ecosystems in the world, and a major portion of the global total is found in Southeast Alaska. In this ecosystem, Sitka black-tailed deer are the dominant large herbivore, influencing large carnivores that prey on deer such as wolves and bears, as well as plant species and communities through browsing. In addition, deer play an important economic and cultural role for humans in Southeast Alaska, making up the large majority of terrestrial subsistence protein harvested each year as well as providing the backbone of a thriving tourism industry built around sport hunting. Given the importance of deer in this system, there remain a surprisingly large number of key gaps in our knowledge of deer ecology in Southeast Alaska.

These knowledge gaps are potentially troubling in light of ongoing industrial timber-harvest across the region, which greatly alters habitat characteristics and value to wildlife. This dissertation research project was undertaken with the aim of filling several connected needs for further understanding deer ecology, specifically 1) patterns of reproduction and fawn survival, 2) population dynamics in response to environmental variability, and the underlying drivers of spatial selection during 3) reproduction and 4) winter. To fill these knowledge gaps, I developed robust statistical tools for estimating rates of fawn survival, and found that fawns must be captured at birth, rather than within several days of birth, in order to produce unbiased estimates because highly vulnerable individuals died quickly and were thus absent from the latter sample. I then use this robust approach to estimate vital rates, including fawn survival in winter and summer, and developed a model of population dynamics for deer. I found that winter weather had the strongest influence on population dynamics, via reduced over-winter fawn survival, with mass at birth and gender ratio of fawns important secondary drivers.

To better understand deer-habitat relationships, I examined both summer and winter habitat selection patterns by female deer. Using summer-only data, I asked how reproductive female deer balance wolf and bear predation risk against access to forage over time. Predation risks and forage were strong drivers of deer spatial selection during summer, but reproductive period and time within reproductive period determined deer reaction to these drivers. To ensure

adequate reproductive habitat for deer, areas with low predation risk and high forage should be conserved. Focusing on winter, I evaluated deer spatial selection during winter as a response to snow depth, vegetation classes, forage, and landscape features. I allowed daily snow depth measures to interact with selection of other covariates, and found strong support for deer avoidance of deep snow, as well as changes in deer selection of old-growth and second-growth habitats and landscape features with increasing snow depth. Collectively, this dissertation greatly improves our understanding of deer ecology in Alaska, and suggests habitat management actions that will help ensure resilient deer populations in the future.

TABLE OF CONTENTS

LIST OF FIGURES

Page

LIST OF TABLES

Page

PREFACE

I am deeply grateful to my major advisor Kris Hundertmark for his guidance, thoughtful discussions, support during challenges of all kinds, and consistent encouragement. I also owe a great deal of thanks to David Person, committee member and extraordinary mentor and in and out of the field, without whom this project, and dissertation, would never have gotten off the ground or through the finish line. In addition, the members of my committee could not have been more helpful- I sincerely thank Mark Lindberg and Mark Boyce for their continuing efforts and insights. Many thanks to all the helping hands in the field, without whom this project would have been impossible. Field assistants Casey Pozzanghera, Kathleen Miles, Tessa Ruswick, and Moira Houghes performed excellent work. Ray Slayton and Jim Baichtal made year-round monitoring of study animals possible, but seemed to enjoy themselves a little too much. In addition, valuable field assistance and logistical support was given by Karen Petersen, Doug Larsen, Rodney Flynn, Boyd Porter, Stephen Bethune, Tim Bartholomaus, and Kris Hundertmark. This research would never have been possible without the love and support of my friends, and of my wonderful husband, Tim Bartholomaus. Cannon the scat detection dog also performed invaluable services, as field assistant and companion, during this work, and is deeply missed. Funding for this work was provided by the Alaska Department of Fish and Game, the U.S. Forest Service, a National Science Foundation GK-12 Graduate Fellowship, an Alaska Trapper Association's Dean Wilson Scholarship, and a Jim Stelmock Memorial Scholarship.

Finally, and importantly, I am deeply grateful for the opportunity to work in the remarkable coastal temperate rainforest ecosystem of Southeast Alaska, and with Sitka black-tailed deer, the consummate forest herbivore. It was a transformative experience, professionally and personally. Perhaps its meaning for me can be best expressed the words of the poet Mary Oliver:

Once, in summer,
in the blueberries,
I fell asleep, and woke
when a deer stumbled against me.

I guess
she was so busy with her own
happiness
she had grown careless
and was just wandering along

listening
to the wind as she leaned down
to lip up the sweetness
So, there we were

with nothing between us
but a few leaves, and the wind's
glossy voice
shouting instructions

The deer
backed away finally
and flung up her white tail
and went floating off toward the trees-

But the moment before she did that
was so wide and so deep
it has lasted to this day;
I have only to think of her-
The flower of her amazement
and the stalled breath of her curiosity,
and even the damp touch of her
solicitude
before she took flight-

To be absent again from this world
and alive, again, in another,
for thirty years
sleepy and amazed,

rising out of the rough weeds,
listening and looking.
beautiful girl,
where are you?

~ Mary Oliver

CHAPTER 1. INTRODUCTION

1.1. GENERAL INTRODUCTION

The coastal temperate rainforest is a rare biome globally (Mackinnon 2003), and a substantial portion of it is found in Southeast Alaska (Albert & Schoen 2013). However, highly productive old-growth forests have been selectively targeted by widespread commercial timber harvest, resulting in disproportionate decreases in high-quality old growth across the region (Albert & Schoen 2007; Albert & Schoen 2013). In this ecosystem, deer (Sitka black-tailed deer, *Odocoileus hemionus sitkensis*) are by far the most abundant large herbivore, and on many islands in the Alexander Archipelago are the only ungulate in the ecological community. Deer depend on high-quality old growth as winter habitat (Schoen & Kirchhoff 1985; Kirchhoff 1994; Parker et al. 1999; Person et al. 2009), due to the high levels of snow interception combined with relatively abundant forage produced by the complex canopy structure (Alaback 1982; Alaback & Saunders 2013; Kirchhoff & Schoen 1987). The widespread changes wrought by timber harvest can strongly affect deer (Hanley 1993; Hanley 2005), although considerable uncertainty remains as to the relationships between deer and habitat types, weather, and predation.

As the dominant large herbivore in the ecosystem, deer are a key member of food webs, feeding bears, wolves and eagles, and consuming a diverse array of plant species. At high densities, Sitka black-tailed deer can substantially alter floral communities by preferentially consuming palatable species (Klein 1965; Le Saout et al. 2014; Stockton et al. 2010; Stockton et al. 2005). Alternatively, when deer are at low densities, predators that rely on them such as the Alexander Archipelago wolf (*Canis lupus ligoni*) may decline or be locally extirpated (Lewis & Klein 1992). Deer also play a key cultural and economic role in Southeast Alaska. In the state, subsistence harvest of wild foods makes up over 30% of calories for rural residents, equating to the harvest of 375 pounds of food per person annually. So important is subsistence harvest to the economy and culture of rural Alaska that it is a legally protected under federal law by the Alaska National Interest Lands Conservation Act (ANILCA). In Southeast Alaska, deer are the major terrestrial source of protein for subsistence users, making up 18% of the total subsistence harvest in Southeast Alaska by weight. Much of this harvest occurs within a mile of the high-density

network of roads across the region (Brinkman et al. 2009), which is the product of industrial timber harvest.

Yet despite the pivotal ecological and cultural role of deer in Southeast Alaska, there remain critical gaps in knowledge for the species, from life history and population dynamics to spatial ecology during key life-history phases. In part, this is because data are profoundly difficult to collect in the temperate rainforest environment. From capture to detecting birth and mortality events, studies of deer are only infrequently facilitated by aids such as helicopters and airplanes due to the thick forest canopy. Despite these challenges, many dedicated researchers have studied deer in Southeast Alaska across recent decades, and have produced high-quality studies of adult female survival and spatial selection. But these studies have limitations, particularly in collection of spatial data. Recent technological advances, specifically the advent of GPS-based wildlife tracking technology, have increased the data that can be collected on deer by orders of magnitude. As new research techniques have emerged during recent years, interest has grown among managers and researchers in filling in key gaps in knowledge regarding deer ecology in Southeast Alaska. My study attempts to use some of those new technologies to fill in gaps concerning the ecology of deer in coastal temperate rainforest.

The goals of my study were to investigate the environmental drivers of adult female and fawn survival, how those factors affected relations between deer and their predators, and patterns of spatial selection by adult females during reproduction and winter. As part of that work, I also tested the utility of a new technology that has the potential to enhance the study of deer reproduction in dense forest environments. In the following sections I describe the background and questions addressed for each chapter of the dissertation.

1.2. CHAPTER 2 BACKGROUND: CHALLENGES IN SURVIVAL ESTIMATION

Despite sustained interest from researchers and managers in Sitka black-tailed deer ecology, our understanding of their population dynamics is quite limited. Although estimates of adult and yearling female survival have been obtained (Farmer et al. 2006; Person et al. 2009), deer reproduction in this ecosystem remains almost entirely unstudied (but see Johnson 1987 for estimates of fetal rates from deer reproductive tracts). Knowledge of timing of reproduction, rates and sex ratios of fawn production, selection of birth sites, survival rates of fawns, and

ecological factors affecting that survival are lacking. For populations of long-lived mammals such as deer, variability in population growth rate between years is typically caused by changes in survival of juveniles, rather than survival of adult females (Gaillard et al. 1998; Gaillard et al. 2000). Without an understanding of processes affecting fawn survival, inference about the ecological drivers of population dynamics of Sitka black-tailed deer is difficult and probably not very reliable.

One obstacle to studying population dynamics is accurate measurement of fawn survival rates. Female deer, like other forest ungulates, are highly secretive as parturition approaches. As a result, many studies of fawn survival rely on opportunistic captures of young fawns that are detected based on female behavior, through direct observation, or by systematic ground searches (White et al. 1972; Whittaker & Lindzey 1999). However, the emergence of a new technology, vaginal implant transmitters (VITs), has allowed researchers to detect fawns at birth. The VIT is expelled from the vaginal canal during labor and then emits a distinctive radio signal, allowing researchers to locate the birth site. By capturing fawns at birth rather than several days after, researchers detect early mortality events that would otherwise have been missed (i.e., left truncation of data; Shen & Cook 2013). In chapter 2, I compare survival of opportunistically and VIT-captured fawns to quantify the importance of this missed mortality to accuracy of survival estimates. This was an important step toward developing accurate models of fawn survival for ecological inference in later chapters.

1.3. CHAPTER 2 RESEARCH QUESTIONS

In this chapter, I address four main research questions:

1. Does the methodology for capture of neonatal fawns introduce bias into the data (i.e., left truncation)?
2. Does left truncation bias survival estimates for fawns and by how much?
3. Does left truncation affect ecological inference?
4. What are potential solutions to left truncation in data?

1.4. CHAPTER 3 BACKGROUND: ENVIRONMENTAL VARIABILITY AND POPULATION DYNAMICS

Building on the robust tools for modeling fawn survival in the presence of biased data developed in Chapter 2, the next chapter focuses on deer population dynamics in a variable environment. Population dynamics of ungulates in temperate environments are affected by multiple environmental factors that vary across seasons and in impacts to vital rates (Gaillard et al. 2000; Monteith et al. 2013). Fecundity is often a function of maternal age and size, as well as the environment (Delgiudice et al. 2007; Weladji et al. 2002). In addition, survival patterns and predictive environmental variables differ by life history phase, with juveniles typically much more vulnerable to predation, malnutrition, and other causes of mortality than adult females (Gaillard et al. 1998). While such general patterns are likely true for Sitka black-tailed deer, the environmental drivers of survival and fecundity are poorly understood. Climate variability, particularly in winter snow depth and temperature, is thought to be important for over-winter survival of adult females and fawns (Baccante & Woods 2010; Kirchhoff 1994; Person et al. 2009, Person & Brinkman 2013). Likewise, timber harvest may have an affect on nutrition or predation risk (McNay & Voller 1995, Fisher & Wilkinson 2005; Van Horne et al. 1988; Farmer et al. 2006, Wittmer et al. 2007, Person & Brinkman 2013). In addition, individual factors, such as mass at birth or gender for fawns or body mass and age of adults, can also influence vital rates (Loison et al. 2004; Delgiudice et al. 2006). To evaluate population growth sensitivity to vital rates and underlying environmental and individual predictive variables, I developed an integrated modeling approach, which combines models of vital rates with matrix-based population models.

1.5. CHAPTER 3 RESEARCH QUESTIONS

In this chapter I use the aforementioned methods to address four main research questions:

1. What are the effects of environmental and individual predictor variables on deer reproduction and survival (i.e., vital rates)?
2. How much of observed inter-annual variance in vital rates can be attributed to process versus sampling variance?
3. What are the potential effects of observed process variance in vital rates on population growth rate?

1) What are the potential effects of observed process variance in predictor variables on population growth rate?

1.6. CHAPTER 4 BACKGROUND: SPATIAL SELECTION DURING REPRODUCTION

Adult female deer have been the focus of research across ecosystems (Delgiudice et al. 2002; Long et al. 2009; Mcloughlin et al. 2006) because they are the segment of the population that produces offspring, and thus in large part drive population growth or decline. Hence, understanding how the reproductive status of female deer drives habitat selection during spring and summer is a central question for effective conservation and management of deer. Whereas past studies have described summer habitat selection by female deer (Kirchhoff & Schoen 1985; Yeo & Peek 1992; Person et al. 2009), reproductive status was not known for individuals. Reproduction involves extreme energy expenditures for adult female deer during gestation and lactation (Barboza & Bowyer 2000; Barboza et al. 2009; Tollefson 2010), as well as changes in predation risk for both females and fawns (Therrien et al. 2008). Distinct changes to habitat selection by reproductive phase has been documented for other female ungulates (Berger 2007; Long et al. 2009; Rearden et al. 2011), but has not been studied in Sitka black-tailed deer. If habitat selection by deer differs by reproductive stage, land management strategies may need to consider habitat quality for deer throughout the year rather than just focusing on winter range. Consequently, I investigated patterns of habitat selection by adult female deer during different reproductive stages. Furthermore, I examined whether those patterns can be explained by risks of bear and wolf predation and forage availability across the landscape.

1.7. CHAPTER 4 RESEARCH QUESTIONS

In this chapter, I examine 3 main research questions:

1. Do adult female deer trade-off bear and wolf predation risk with access to forage during reproduction?
2. Does duration of a reproductive phase affect deer choices relative to risk and forage?
3. Do deer exhibit a functional response in strength of selection dictated by the levels of risk and forage available to them within their home ranges?

1.8. CHAPTER 5 BACKGROUND: EFFECTS OF SNOW ON SPATIAL SELECTION

There is ongoing debate as to the habitat needs of Sitka black-tailed deer in winter. The importance of winter to deer survival in Alaska has long been recognized, and several previous studies have sought to identify key habitats for deer in winter (Doerr et al. 2005; Farmer et al. 2006; Klein 1965; Person et al. 2009; Schoen & Kirchhoff 1985; Yeo & Peek 1992). A unifying question across these studies has been the importance of productive old-growth forest to deer in winter, an issue with great importance as old-growth timber continues to be harvested across the region. While old growth harvest has slowed in recent years (U.S. Forest Service 2008), the remaining stands of high-quality old growth could arguably have greater importance for deer due to the relative scarcity of these habitat types (Albert & Schoen 2007).

Yet past studies fail to agree on the importance of old growth. One explanation is that the value of old growth to deer depends on snow depth, with productive old growth most valuable when snow is deep and other habitats with adequate forage are snow covered. However, the highly variable winter climate in Southeast Alaska means that snow depth changes throughout the winter, and across latitudinal and elevational gradients (Shanley et al. 2015), confounding efforts to distinguish effects of snow depth on deer selection. It is urgent that the discrepancies in results of past studies be reconciled in order to ensure the preservation of high-quality deer habitat for both deep and shallow snow conditions. To disentangle snow and habitat effects on deer selection, I used GPS-obtained locations for deer with high temporal and spatial resolution and data from weather stations deployed throughout the study area to measure snow depth daily, and closely monitored deer movements and habitat selection during winter.

1.9. CHAPTER 5 RESEARCH QUESTIONS

In this final research-based chapter, I answer the following three research questions:

1. What landscape, vegetation, and forage covariates do deer select for or against in winter?
2. How does variability of snow depth affect these selection patterns?

1) Do deer adjust selection for vegetation classes and biomass based on what is locally available to them?

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Figure 1.1. Photo of the Author Opportunistically Capturing a Sitka Black-Tailed Deer Fawn Capture took place in the project study area on Prince of Wales Island, Southeast Alaska during the 2010 summer field season.

CHAPTER 2. DEAD BEFORE DETECTION: ADDRESSING THE EFFECTS OF LEFT TRUNCATION ON SURVIVAL ESTIMATION AND ECOLOGICAL INFERENCE FOR NEONATES[1]

2.1. ABSTRACT

Neonate survival is a key life-history trait, yet remains challenging to measure in wild populations because neonates can be difficult to capture at birth. Estimates of survival from neonates that are opportunistically captured might be inaccurate because some individuals die before sampling, resulting in data that are left truncated. The resulting overestimation of survival rates can further affect ecological inference through biased estimates of covariate effects in survival models, yet is not addressed in most studies of animal survival. Here, I quantify the effects of left truncation on survival estimates and subsequent ecological inference. Vaginal implant transmitters (VITs) enable capture of ungulates at birth, yielding data without left truncation. The effects of left truncation on survival estimation were quantified using age-dependent survival models for VIT and opportunistically captured neonatal deer. Differences in daily survival rates (DSRs) and cumulative survival probability were calculated for the first 70 days of life. In addition, left truncation was simulated by removing fawns that died during the first 1 or 2 days of life from the VIT-caught sample, isolating the effect of left truncation. Cumulative probability of survival during the first 70 days of life was overestimated by 7- 23% for fawns caught opportunistically compared to those caught by VIT, depending on model design. Differences in DSRs were large at age 1 day, but had converged by age 30 days. Simulated left truncation resulted in overestimates of survival of up to 31%. Model selection and covariate coefficients were strongly affected by left truncation, producing spurious ecological inference, including changes to sign and/or magnitude of inferred effects of all covariates. I recommend 1) every effort be made to

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[1] Gilbert SL, Lindberg MS, Hundertmark KJ, Person DK (2014). Dead before detection: addressing the effects of left truncation on survival estimation and ecological inference for neonates. Methods in Ecology and Evolution, 5(10), 992-1001. DOI: 10.5061/dryad.p1r40. The text has been modified to conform with thesis formatting requirements.

capture neonates; 2) consistent capture methods, using at least in part non-truncating techniques, be implemented across years and study areas; and 3) exclusion of left-truncated data from survival estimates until DSRs converge with those calculated from non-truncated data. This work emphasizes the importance of accounting for left truncation in survival estimation for any species with strong age-dependent survival in order to prevent biased conclusions produced by sampling method rather than true ecological effects.

2.2. INTRODUCTION

Neonatal survival is a key ecological metric, driving the reproductive success of individuals and subsequent population change. For most vertebrates, the neonatal period immediately following birth of offspring or laying of eggs is the highest risk life history stage (Gaillard et al. 1998; MacNulty et al. 2009) Yet quantifying neonatal survival remains elusive for many species, largely due to challenges in early detection and capture of neonates (Pike et al. 2008; Shemnitz et al. 2012) which is my focus, or the laying of eggs. This failure to detect truly neonatal individuals results in longitudinal survival data that are left truncated, and inference is therefore based on the sample of individuals that have survived to be detected and captured (Tsai et al. 1987; Heisey & Patterson 2006).

Neonatal survival is typically estimated by closely monitoring marked adults during the reproductive period, using behavioral cues to detect reproduction, and then searching for offspring, nests or dens (White et al. 1972; Laurenson 1994; Safine & Lindberg 2008; Shemnitz et al. 2012). Age of detected offspring or nests is then determined so that age-specific survival rates can be calculated, and survival outcomes monitored (Dinsmore et al. 2002). This approach introduces error into survival estimates both when offspring age is estimated using imperfect proxy measurements (Haskell et al. 2007) and when some neonates or nests die or fail before detection (i.e. left truncation, Fieberg & DelGiudice 2009). Although researchers can estimate the error in age determination of offspring or nests (Carstensen et al. 2009), estimation of or correction for the effects of left truncation are rarely attempted.

Increasingly, survival estimation is not the sole goal of research, but rather is a necessary component of subsequent analysis, such as modeling of ecological, genetic or

behavioral drivers of survival. Left truncation can inflate estimates of neonatal survival and bias estimated effects of covariates (Fieberg & DelGiudice 2009; van den Berg & Drepper 2011; Yang & Aldrich 2012). When using left-truncated data for survival estimation, environmental or individual covariate values associated with these data are incomplete because they only come from individuals that have survived to be sampled, resulting in biased estimation of covariate effects (Bergeron et al. 2008; Shen & Cook 2013). Accurate data on timing of mortality and effects of covariates are essential, and left truncation should therefore be a serious consideration in study design.

Progress has been made in incorporating individual heterogeneity into survival models in recent years and analytically accounting for many sources of variation in neonatal survival. From the Mayfield nest survival estimator (Mayfield 1961), which assumes a constant daily survival rate (DSR) throughout the nesting cycle in order to account for differing times of exposure to mortality risk, researchers have progressed to explicitly modeling the effects of nest age (Rotella et al. 2004) and variation in individual quality (Lindberg et al. 2013). Such sophisticated survival models have also been applied to other vertebrate taxa in recent years (Keech et al. 2011; Halstead et al. 2012). Yet if low-quality individuals are removed disproportionately at very young ages, as is often the case in vertebrate populations, the data driving these models are left truncated and biased towards high-quality individuals. Therefore, none of these modeling solutions account for the sampling problems associated with left truncation.

Left truncation bias for neonates is primarily a sampling rather than a modeling problem. However, recent technological innovations present an opportunity to quantify the effect of left-truncated data on survival estimation and to develop approaches to successfully integrate truncated and non-truncated data into survival models. For instance, vaginal implant transmitters (VITs; Advanced Telemetry Systems, Isanti, MN, USA) have proven highly useful in the study of ungulate reproduction. VITs use a temperature-based switch linked to a VHF radiotransmitter to signal researchers when the transmitter is expelled during birth from the relatively warm body of a female ungulate into cooler air temperatures. In this way, VITs have allowed for the location of birth sites and neonates even for highly cryptic species such as white-tailed deer (*Odocoileus virginiaumus*; Carstensen et al. 2003; Swanson et al. 2008), mule deer (*Odocoileus*

hemionus; Johnstone-Yellin et al. 2006; Haskell et al. 2007; Bishop et al. 2011) and elk (*Cervus elaphus* ; Seward et al. 2005; Barbknecht et al. 2009).

Currently, VITs are seen by most researchers as a method to improve capture efficiency, rather than to increase accuracy of survival estimates by reducing left truncation (Carstensen et al. 2003; Haskell et al. 2007). Indeed, most studies of neonate survival either do not use VITs or use a mixture of VITs and opportunistic captures across years and study areas without accounting for the effects of these two detection methods on survival estimation. Differences in estimates of offspring survival between VITs and opportunistic capture methods are likely, because newborn ungulates are highly cryptic in many species, becoming more active and detectable and less vulnerable to predation as they age (Gaillard et al. 1998; Forrester & Wittmer 2013; Van Moorter et al. 2009). To quantify the effect of left truncation on neonatal survival estimation and modeling of ecological covariates, I compared neonatal survival in a population of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) sampled concurrently using both VIT and opportunistic capture methods.

2.3. MATERIALS AND METHODS

2.3.1. Study Area

Our study area was located on central Prince of Wales Island, the largest island in the Alexander Archipelago of Southeast Alaska (Figure 2.1). The regional ecosystem is a coastal temperate rain forest, and the watersheds within the study area, along with the majority of land in Southeast Alaska, are part of the Tongass National Forest. Precipitation, falling mostly as rain, averages 300 cm per year. Temperatures vary moderately annually, although deep snow (>50 cm) can accumulate during winter months (Shanley et al. 2015). Habitat composition is naturally quite variable, including several types of old-growth forest, abundant riparian, estuarine and lacustrian environments, and muskeg heaths.

In addition, widespread clear-cut logging has produced single cohort, even-aged forest stands of differing successional stages throughout much of central Prince of Wales Island, resulting in a patchwork distribution of altered and unaltered habitat in many watersheds (Alaback 1982; Alaback & Saunders 2013). I selected six watersheds in the

central portion of Prince of Wales Island to examine survival of Sitka black- tailed deer, three of which were heavily harvested for timber and three that had no timber harvest within them.

2.3.2. Deer Capture and Handling

A total of 54 adult female deer were captured in April and May during 2010 – 2012. Each deer was fitted with a GPS collar with mortality sensor, measured to determine body size and condition and fitted with a VIT if pregnant. Pregnancy was assessed using a portable ultrasound machine (Sonosite Titan, Sonosite, Bothel, WA, USA). VITs had temperature switches triggered by expulsion at birth, producing a birth signal at temperatures below 35 °C. VITs were monitored twice daily, and ground searches for birth sites were initiated immediately upon detection of a VIT birth signal. If a VIT signal could not be detected (i.e. a female was outside of the VIT transmission range of c. 1 km), vehicle and aerial searches were conducted until the female was relocated. Birth sites found using VITs were confirmed based on presence of birth fluids, proximity of female and presence of fawns. If fawns were not found immediately at the birth site, a fawn search was initiated in the vicinity for at least 2 h, or until two fawns were detected.

In addition to fawn captures using VITs, I opportunistically captured neonatal fawns encountered along roads or otherwise encountered in the environment. Fawns were approached on foot and gently restrained in a mesh sack with eyes covered. Gloves were worn while handling fawns, and handling times were <10 min per fawn. Each fawn was fitted with an expandable radiocollar (VHF, or GPS with VHF; Advanced Telemetry Systems, Isanti, MN, USA) and measured to determine mass, chest girth, body length, hind foot length and new hoof growth. Radiocollar marking of fawns does not cause abandonment by mothers (Powell et al. 2005). VHF signals from fawn collars were monitored 1–2 times per day from birth until August 1st and approximately twice per month through the first year of life. New hoof growth was not measured during 2010, and as a result, fawn survival analysis presented here includes only fawns captured during 2011–2012. Seventy-six fawns were captured opportunistically (n = 40 in 2011, n = 36

in 2012) and 31 from collared females fitted with VITs (n = 15 in 2011, n = 16 in 2012), for a total of 107 fawns during this 2-year period.

2.3.3. Survival Analysis

Fawn Ages and Individual Covariates

I estimated the age of opportunistically captured fawns using two different approaches that have been employed in previous studies. First, I used a published hoof growth equation for mule deer that uses new hoof growth (i.e. length of hoof above the cuticle line, which indicates growth of hoof since birth) as a proxy for age, based on a linear relationship between age and hoof growth from sequential re-measurement of captive-raised (Robinette et al. 1973) or VIT-caught wild fawns (Haskell et al. 2007). New hoof growth is the most commonly used method for estimating age of opportunistically captured fawns (Lomas & Bender 2007; Grovenburg et al. 2011). However, the accuracy of estimates produced for very young fawns can be <50% (Sams et al. 1996; Carstensen et al. 2009), indicating that this metric may be too variable for use in neonatal-focused survival studies. In addition, choice of hoof growth equation can affect model selection among fawn survival models (Grovenburg et al. 2014). I use this technique because it is ubiquitous in the literature and serves as a comparison with other age determination techniques. I used the hoof growth regression equation developed by Haskell et al. (2007) for determining age of mule deer fawns, as this is the only published equation based on wild, VIT-caught individuals of the study species.

Due to the fact that no hoof growth equation exists for the Sitka black-tailed deer subspecies, and because fawns caught opportunistically were thought to be quite young based on behavioral and morphological characteristics (Haugen & Speake 1958), I suspected that the accuracy of hoof growth equation might be too low given the study questions. Subsequently, I used an additional technique for age determination for comparison. I empirically developed a capture age window based on recaptures of VIT-caught fawns (i.e. fawns of known ages) and assigned the midpoint of this empirical capture window as the age of opportunistically captured fawns (Johnson et al. 2004; Whiting et al. 2008). The oldest age at which recapture was successful was 10 days,

which I used as a maximum age for fawns caught opportunistically. I then assigned the midpoint age of 5 days to all opportunistically captured fawns. I therefore had two different estimates of age at capture for fawns caught opportunistically, which in turn yielded two versions of the age-dependent individual covariates for survival analysis (i.e. birth date and birth mass). I calculated birth date by subtracting age at capture from capture date. Mass at birth was calculated based on an assumption of a linear relationship between mass and age, with age predicting mass through a daily mass gain (i.e. slope) of 0.195 kg/day (Anderson 1981).

Survival Models

I examined the effect of left truncation (i.e. capture method) on fawn survival estimates using a set of nest-survival models with a logit link function in program MARK (White & Burnham 1999), which allowed us to consider effects of covariates that varied on a daily basis (e.g. fawn age) that might have a large effect on fawn survival. Analysis was carried out using the program Rmark (Laake 2013), implemented in the R statistical framework (R Development Core Team 2014). To account for potentially confounding individual covariates and explore effects of truncation on ecological inference, I included fawn sex, birth date, timber harvest regime of watershed, mass at capture and year into the full survival model. I also examined a set of survival models composed of combinations of the age-dependent covariates (fawn age, date of birth and mass at capture) because I specifically wanted to quantify the effects of ageing techniques and left truncation on survival estimation.

The goal of model development was to quantify the effect of left truncation on survival estimation and ecological inference and to isolate the effect of left truncation from that of age estimation technique. To do this, I ran a set of survival models across a range of left-truncation levels created using VIT and opportunistically caught fawn data, with model structures that used VIT-only data (least truncation), separated these data, combined data with-group effect, and combined data without-group effect. I then simulated left truncation using VIT-only data to isolate the effect of left truncation from that of age estimation technique.

First, to create baseline survival models that contained no left truncation, I developed a set of nine models using data solely from VIT-caught fawns. Because all fawns within this data set were caught at birth, these models also were free from the effects of age determination techniques. I then quantified the effect of left truncation alone using simulations of left truncation. In the simulations, the VIT-only data were reduced systematically by first removing all fawns that died within the first day of life (n = 7), then those that died at 2 or fewer days old (an additional three fawns). I did not continue this simulation beyond 2 days, as the sample size would be too greatly diminished to support the full covariate model. To explore left truncation with empirical rather than simulated data, I compared the baseline VIT-only models to models using (a) fawns caught opportunistically (hereafter, opportunistic only), quantifying the specific effects of left-truncated data; (b) combined opportunistic and VIT-caught fawns without-group model structure (hereafter, combined without group), quantifying the effects of combining left truncated and untruncated data; and (c) combined VIT and opportunistic fawns with group structure (hereafter, combined with group), quantifying the effects of combining left truncated and untruncated data, but with appropriate model structure. For comparisons (b) and (c), which used fawns caught opportunistically, I developed two versions of each model based on the two age estimation techniques. Finally, I examined model rankings based on AICc scores (Burnham & Anderson 2002), as well as changes in beta coefficients of covariates in the full covariate model, for comparisons (a), (b) and (c).

The full covariate models were used to produce daily survival rates (DSRs) and cumulative survival probabilities for the neonatal period, across the comparisons and simulations. From each version of the full covariate model, I derived DSRs and cumulative survival probabilities for 1–69 days of age. DSRs were produced by varying the value of the age covariate from 1 to 69 days while holding other covariates at mean values, allowing us to project the effect of age from day 1 onwards even for opportunistically captured fawns (i.e. extrapolation of survival intercept from beta coefficient slope). Then, I calculated cumulative survival probabilities for each full model by multiplying DSR estimates for ages 1–69 days. Mean, standard errors and 95% confidence intervals for cumulative survival probabilities were estimated using 1000 non-

parametric bootstrapped replicates of each model (Buckland & Garthwaite 1991), implemented in the R package Boot (Cantey & Ripley 2013). For the combined with-group models, bootstrap resampling was implemented within VIT/opportunistic strata (Cantey & Ripley 2013).

2.4. RESULTS

2.4.1. VIT Success Rates

Of the adult female deer captured, 51 were determined to be pregnant at the time of capture and 49 were successfully fitted with VITs. Two other deer were pregnant but vaginal diameter was too small to accommodate the vaginoscope used in implanting the VITs. Of the 49 deployed VITs, 81% resulted in confirmed birth sites and 62% in captured fawns at the birth site, representing very high retention and fawn detection rates in comparison with other VIT-based studies (Bishop et al. 2011). In addition, 8% of females fitted with VITs expelled the devices before parturition, identified by VITs found at sites lacking the characteristics of birth sites.

2.4.2. Survival Analysis

Fawn Age and Age-dependent Covariate Estimation

The mean value of measured new hoof growth for opportunistically captured fawns was 2.64 mm (*SD* = 1.51) and included 16 fawns for which no new hoof growth was observed (i.e. <24 h old), confirming that many fawns were quite young at capture. However, many of the age estimates produced by the hoof growth equation were higher than the 1–10 day-old plausible capture window from the field study (Mean = 10.4, *SD* = 3.77), with a minimum age estimate of 5.29 days. To generate more realistic age estimates, I subtracted 5.29 days of age from the distribution produced by the hoof growth equation, so that the youngest age estimates were 0 days, and all other ages were 5.29 days younger (Table 2.1). This adjustment produced a new mean age of 5.12 days (*SD* = 3.77). In contrast, the empirical capture window approach resulted in uniform, 5-day-old fawn ages at birth, masking true variation in fawn age at capture but producing plausible fawn ages relative to the empirical capture window without the need for adjustment.

These differences in estimated age-at-capture between age determination techniques resulted in variation in derived, age-specific covariate values (i.e. mass at birth and birth date) for opportunistically captured fawns (Table 2.1). The fawn ages generated by the hoof growth equation and empirical capture window techniques both resulted in underestimates of mean mass at birth relative to VIT-caught fawns, but generated a mean birth date equal to that of the VIT-caught fawns. This might indicate that the 0.195 kg/day rate of mass gain that I used to estimate mass at birth was too high for this very small subspecies of mule deer, but that fawn ages are likely fairly accurate.

Survival Estimates

The varying levels of left truncation within the VIT-only data, opportunistic-only data, combined data without groups, combined data with groups and simulated-truncation data resulted in different DSRs and cumulative survival rates (Figs 2.2 and 2.3). The separated models based on opportunistic-only data produced estimates of DSRs and cumulative survival probability that were higher than those based on VIT-only data; Cumulative survival probabilities from opportunistic-only data were 0.40 ($SE = 0.13$) when the hoof growth regression equation was used and 0.44 ($SE = 0.08$) when the empirical capture window approach was used. In contrast, estimates of cumulative survival probability from VIT-only, untruncated data were 0.33 ($SE = 0.13$).

Combining opportunistic and VIT-caught fawn data without-group structure resulted in DSRs and cumulative survival probabilities that were slightly higher than those of the VIT- only model, resulting in cumulative survival estimates of 0.35 ($SE = 0.19$) using hoof growth regression-based age estimates and 0.36 ($SE = 0.20$) using the empirical capture window approach to age estimation.

As expected, when groups were used to control for VIT and opportunistic differences, opportunistically caught groups had higher cumulative survival probabilities than VIT-caught groups (Table 2.2), produced by large differences in DSR at 1 day of age that converged to no difference in DSR after approximately 30 days of age (Figure 2.2). For the model that used age estimates from the hoof growth equation, across-group cumulative survival probability was 0.33 ($SE = 0.06$); DSRs for opportunistic groups relative to VIT groups were higher until approximately 24 days of age, producing

cumulative survival probabilities of 0.40 (*SE* = 0.08) and 0.25 (*SE* = 0.11), respectively. When the empirical capture window was used to generate age estimates, across-group cumulative survival probability was 0.35 (*SE* = 0.07). DSRs converged at approximately 35 days of age (Figure 2.2), with cumulative survival probabilities of 0.46 (*SE* = 0.09) and 0.23 (*SE* = 0.11) for the opportunistic and VIT groups, respectively.

Models that used simulated left-truncation data, through removal of VIT-only fawns that died in the 1st and 2nd days of life, resulted in cumulative survival probabilities that were progressively higher depending on level of truncation, and higher than for any other models. Removal of fawns that died during the first day of life resulted in an increase in cumulative survival probability to 0.55 (*SE* = 0.21), and removal of fawns that died during both the first and second days of life increased cumulative survival probability to 0.64 (*SE* = 0.28). These increases in cumulative survival were the result of increased DSRs at young ages (Figure 2.2), resulting from an underestimation of the effect of age on survival (Table 2.3, Figure 2.4).

Effects of Truncation on Model Selection

Model selection based on AICc scores differed depending on the level of left truncation in the data. The opportunistic-only and VIT-only models selected quite different top models (Table 2.4); the top-ranked model based on the VIT-only model structure was the full covariate model, including effects of age, birth mass, birth date, sex, timber harvest and year, and no other models were within 2 AICc units when using VIT-only data. This model was not within 2 AICc units of the top-ranked model when using opportunistic-only data, based on either age estimation approach.

The combined VIT and opportunistic model structures, with or without groups, also disagreed with model rankings of the VIT-only model, instead selecting simpler models with fewer covariates than the full covariate model. The two versions of this model structure, based on age estimates from hoof growth regression and the empirical capture window, both yielded a top-ranked model that included age, birth mass and birth date as covariates (Table 2.4) and agreed on a joint model set within 2 AICc units of this best model. The combined, group-controlled model structure resulted in model rankings identical to that of the without-group structure. The simulations of left truncation resulted

in a top-ranked model that included all covariates (i.e. the full model) for both levels of the simulated truncation (i.e. –1 and –2 days of mortality), although the simulation missing only 1 day of mortality selected two other models within 2 AICc units, whereas the simulation missing 2 days of mortality included only the full covariate model.

Effects of Truncation on Ecological Inference

Model structure also strongly influenced the estimated effects of individual and environmental covariates (i.e. beta coefficients) in survival models. These alterations to coefficients included changes to both magnitude of coefficients, in which a small effect became a large effect or vice versa, and sign of coefficients, in which a positive effect on survival became a negative effect or vice versa.

Model structure therefore resulted in quite different ecological inference even when considering the full model, which included age, birth mass, birth date, sex, timber harvest regime and year covariates. In general, the more left truncation present in a given model structure, the greater the differences in coefficients between that model structure and the non-truncated, VIT-only model structure (Figure 2.4). Left truncation in the data progresses from no truncation in the VIT- only data, through the combined data with groups, combined data without groups, opportunistic-only data and finally simulated-truncation data.

Across this gradient of left truncation, the effect of age on survival consistently declined from a strongly positive effect in the VIT-only model, through diminishing positive effects in the with-group effect, combined and opportunistic-only models, to a marginally positive effect in the simulated-truncation models. The effect of birth date (i.e. being born at a later julian date) consistently increased from a slightly negative effect to a positive effect on survival through this same gradient of models. The effect of birth mass changed in a nonlinear fashion, declining from a strongly positive effect on survival in the VIT-only model to a weakly positive effect in the with-group effect and combined models and a neutral effect in the opportunistic-only model, then increasing to a strongly positive effect in the simulated model structures. The effect of year declined steadily along the left-truncation gradient, from a strongly positive effect of the year 2012 over year 2011, to a neutral effect. The effect of sex changed in a nonlinear fashion, with a

strong negative effect of male gender on survival for the VIT-only model changing to a neutral effect of male gender for grouped- controlled, combined and opportunistic-only structures, with a negative effect re-emerging for both simulated-truncation models. Timber harvest within a watershed had a marginally negative effect on survival in the VIT-only model, yet this effect steadily reversed through the truncation gradient, ending with a strongly positive effect on survival in the simulated-truncation models (Figure 2.4).

2.5. DISCUSSION

I found substantial differences in daily and cumulative survival estimates between fawns caught opportunistically and VIT-caught fawns. Simulated left truncation of individuals that died at ages 1 and 2 days resulted in dramatic increases in DSRs and subsequently in cumulative survival compared with untruncated data, greater than differences found in the empirical data. This indicates that left truncation in data can bias survival estimates, even at low levels, if age has a large effect on survival. When I used only empirically left-truncated data, stemming from opportunistic capture of neonatal fawns, DSRS were overestimated up until approximately 30 days of age, and there was a positive bias in cumulative survival probabilities of 0.07–0.23 (SE = 0.15, 0.14) depending on which model design and age estimate was used.

Perhaps even more significantly, ecological inference was heavily biased by left truncation, both during model selection based on AICc ranking, and through large differences in beta coefficients of covariates. Using the untruncated VIT-only data, the full covariate model was the only model selected based on AICc score; In this model, there are strong positive effects on fawn survival of increasing age and birth mass, and increased survival in the year 2012. In contrast, male gender, increasing julian birth date and presence of timber harvest in a watershed had negative effects on fawn survival. Yet had I used a combination of truncated and untruncated data, a simpler top-ranked model would have been selected based on AICc, with age remaining as a covariate but with a diminished positive effect size, birth mass retaining only a marginally positive effect, increasing julian birth date reversing coefficient sign with a positive effect on survival,

and all other covariates excluded. The errors in ecological inference would be further magnified had I used only left-truncated data.

From the level of left truncation in the opportunistic-only data and simulations, which is by no means extreme or unrealistic in terms of real-world sampling age for neonatal animals, the erroneous conclusion would be that age had only a mild positive effect on survival, that increasing julian birth date positively rather than negatively effected survival, that year had no effect at all and that timber harvest within a watershed produced a strongly positive rather than a negative effect on fawn survival. Conclusions reached from any of these levels of left truncation would not only be incorrect ecologically, but would likely negatively impact management of the species, for instance through the falsely positive effect of timber harvest on fawn survival in all models including left-truncated data.

The origins of these biases in coefficients and model selection could be the result of interactive effects with age. For example, timber harvest and birth date might strongly negatively influence survival of fawns during the first few days after birth but positively affect survival as they become older. Ultimately, left truncation is the product of individual survival outcomes early in life and is thus likely dependent on individual quality. Low-quality offspring are likely more susceptible to predation (Lindberg et al. 2013; Reid et al. 2010), and a portion of them die before opportunistic sampling can occur. Low-quality offspring are likely the result of low-quality or inexperienced reproductive adults, which occupy poor birth site, nest, den or home-range habitat, or are unable to provide sufficient nourishment or protection to offspring (Mcloughlin et al. 2006; Hamel et al. 2009). Here, I estimated that the effect of VIT-based captures (i.e. group effect) on survival was on average –0.55 (SE = 0.39) across the age determination techniques, which could be seen as a measure of the difference in frailty between the VIT and opportunistically caught groups. Several mechanisms could be responsible for this difference in frailty and bear further investigation. During this study, numerous females lost fawns at or shortly after birth, indicating that birth site and subsequent habitat selection by females may play a large role in determining fawn predation risk. Future work focusing on the underlying mechanisms through which individual heterogeneity produces differences in fitness could elucidate such processes. The effects of left

truncation I document here have important implications for ecological studies of recruitment, survivorship and population dynamics, particularly those that employ capture-mark-recapture or known-fates estimation of survival that rely on opportunistic, uneven-aged sampling of organisms. Because I captured fawns using left-truncating and non-truncating methods concurrently and in the same geographic area, I were able to estimate the magnitude and persistence of survival differences resulting from left truncation of data; many studies do not have this luxury, yet assume survival is equivalent for animals caught with varying capture methods or that ecological conclusions are sound despite being based on truncated data. I emphasize the need to examine these assumptions empirically.

Survival rates are often the basis for demographic analysis and for making decisions about managing populations (Eberhardt et al. 1994; Beissinger et al. 1998; Servanty et al. 2011). If left truncation is present but not accounted for, results could be spurious and highly misleading for ecologists and managers. However, I suggest that truncated and non-truncated data can be successfully combined within survival models with minimal impact to survival estimation and inference, provided certain guidelines are followed. Left truncation is fundamentally a sampling problem, and the level of left truncation before capture can occur will likely vary by study, by year and by species. Thus, it is key to acquire a subsample of study data from minimally truncated individuals, despite the higher costs of these data, for comparison with more truncated data. This allows for empirically based adjustments of the risk set at a given time, based on the convergence of age-dependent survival rates, with more truncated data only included once age-dependent survival rates have converged. Specifically, I recommend that (i) every effort is made to capture truly neonatal individuals for at least a portion of the sample; (ii) consistent capture methodology, consisting of either non-truncating or a balanced mixture of non-truncating and truncating techniques, is used across years and study areas; and (iii) left-truncated data should be excluded from age-dependent survival estimates until DSRs converge with those calculated from non-truncated data.

2.6. ACKNOWLEDGEMENTS

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2.7. FIGURES

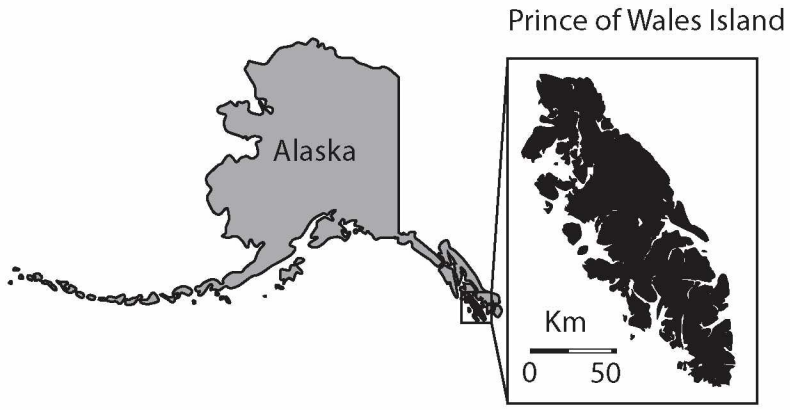

Figure 2.1. Study Area Map

The study area, located on central Prince of Wales Island in Southeast Alaska. Study area consisted of three watersheds where substantial timber harvest has occurred and three watersheds where no significant timber harvest has occurred. Fawns were captured in 2011– 2012, with and without VITs in approximately even numbers across these six study areas.

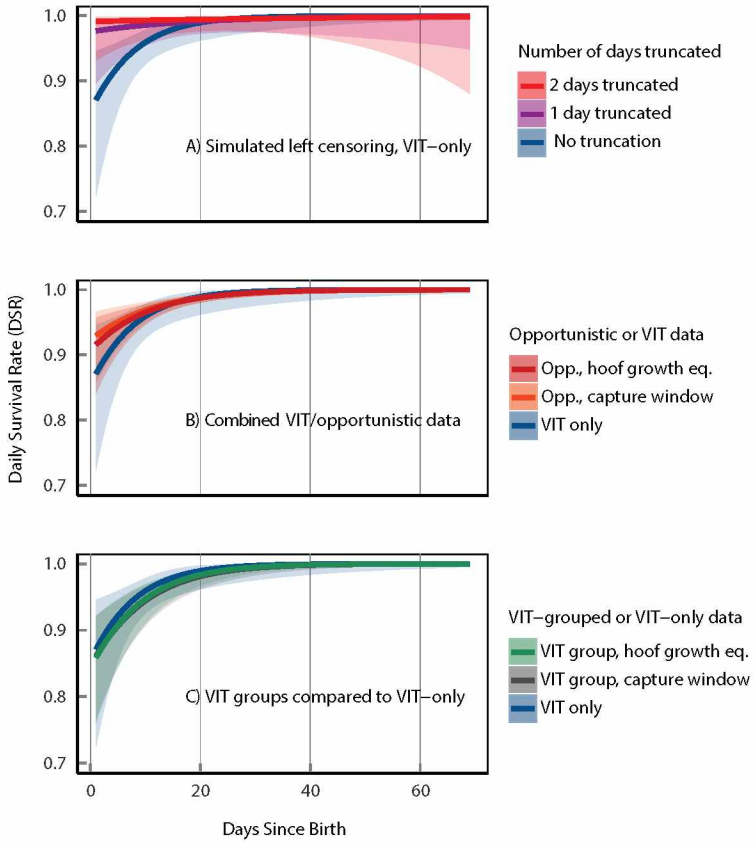

Figure 2.2. Daily Survival Rates (DSRs) for Neonatal Fawns

Estimates are shown from 1 to 70 days old, with means and 95% confidence intervals. (a) Effects of simulated left censoring using VIT-caught fawns, excluding no fawns, fawns that died at <1 day old and fawns that died at <2 days old; (b) effects of maximum left censoring in the data set (only opportunistic individuals), compared with VIT-caught fawns; and (c) differences between estimates from VIT groups and VIT-only model. The full covariate model (S ~ Age + Mass + Birthdate + Sex + Timber + Year) was used to generate all estimates.

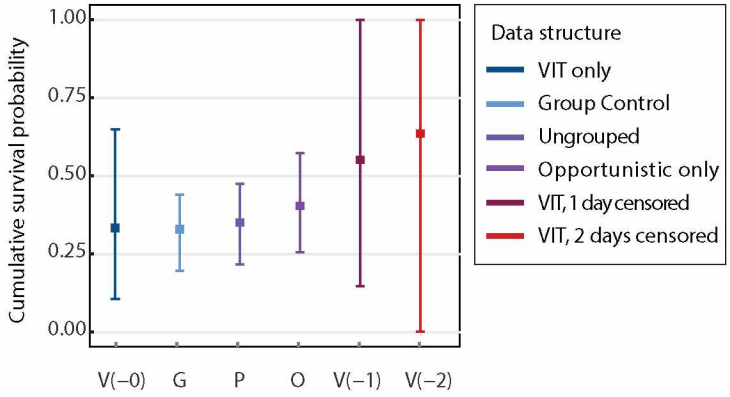

Figure 2.3. Cumulative Survival Probabilities for Neonatal Fawns

Estimates are shown from 1 to 70 days old with means and 95% confidence intervals. The gradient of left censoring effects is explored using both empirical and simulated data, from VIT with 0 days censored, to means of grouped VIT/opportunistic model, pooled model, opportunistic only model, VIT with 1 day censored and VIT with 2 days censored. Opportunistic fawn ages were generated from the Hoof growth equation (2007) age estimation equation. The full covariate model (S ~ Age + Mass + Birthdate + Sex + Timber + Year) was used to generate all estimates.

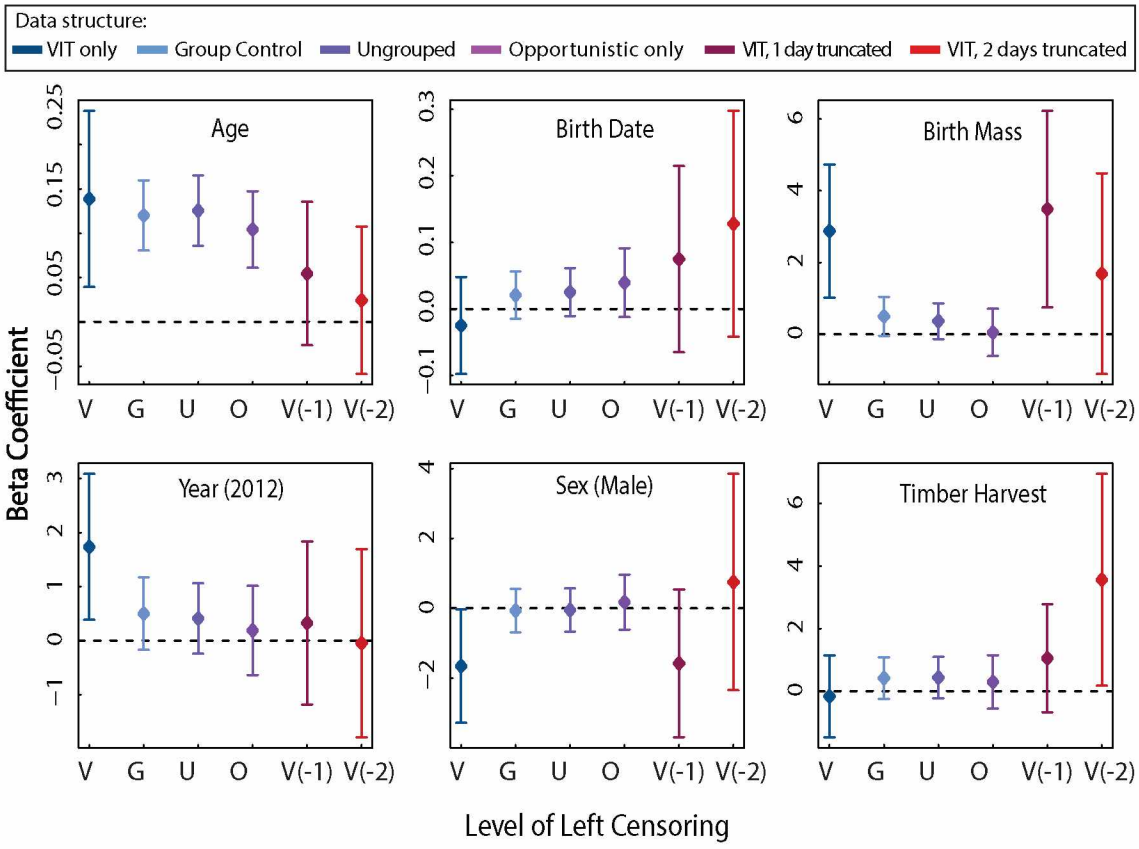

Figure 2.4. The Effect of Left Truncation on Coefficient Magnitude and Direction Coefficients are shown for the full covariate model (S ~ Age + Mass + Birthdate + Sex + Timber + Year) across a gradient of left censoring in each panel, from no censoring using only VIT- caught fawns [V(−0)], through grouped (G), pooled (P) and opportunistic (O) models based on empirical VIT and opportunistic data, to simulations based on VIT-only fawns with left censoring [fawns that died at <1 day removed, V(−1), and <2 days removed, V (−2)].

2.8. TABLES

Table 2.1. Effects of Age Estimation Technique on Covariate Calculations

Differences in estimates of age-dependent covariates resulting from choice of age estimation technique, and p-values of comparison of distributions from fawns caught at birth (i.e., VIT caught fawns) using Welch two sample t-test. Techniques used were 1) hoof growth equation, from Haskell (2007), and 2) an empirically-generated capture window, from this study.

Variables	Age estimation technique	Mean	*SE*	*P* value
Age at capture (days)	Hoof growth equation	5.12	3.77	--
	Capture window	5.00	0.00	--
Mass at birth (kg)	Hoof growth equation	2.18	0.66	0.001
	Capture window	2.17	0.78	0.003
	VIT (caught at birth)	2.57	0.47	--
Birth date (Julian date)	Hoof growth equation	160.33	10.21	0.799
	Capture window	160.44	9.80	0.835
	VIT (caught at birth)	160.90	10.31	--

Table 2.2. Effects of Age Estimation Technique on Covariate Calculations
Left truncation in survival data produces differences in cumulative survival probability from 1 to 70 days of age, based on the model S ~ Age + Mass + Birthdate + Sex + Timber + Year with mean values of covariates. A-E indicate level of truncation, from lowest to greatest. S(Both) indicates estimates from combined opportunistic and VIT data, and S(VIT) and S(VIT) and S(Opp) indicate estimates based on VIT- or Opportunistic-only data.

Model structure	Age estimation	S(Both)	*SE*	S(VIT)	*SE*	S(Opp)	*SE*
A. VIT only	--	--	--	0.33	0.13	--	--
B. Combined, with group	Hoof growth eq.	0.33	0.06	0.25	0.11	0.40	0.08
	Capture window	0.35	0.07	0.23	0.11	0.46	0.09
C. Combined, without group	Hoof growth eq.	0.35	0.07	--	--	--	--
	Capture window	0.36	0.08	--	--	--	--
D. Opportunistic only	Hoof growth eq.	--	--	--	--	0.40	0.09
	Capture window	--	--	--	--	0.44	0.08
E. Sim, -1 day	--	--	--	0.55	0.21	--	--
Sim, -2 day	--	--	--	0.64	0.28	--	--

Table 2.3. Effects of Varying Levels of Left Truncation on Covariate Coefficients in Survival Models

Comparison of beta coefficients from the survival model, S ~ Age + Mass + Birthdate + Sex + Timber + Year, for truncation. A–E indicate level of truncation, from least to greatest.

	Variable (*SE*)					
Model structure	Age	Mass	Birthdate	Sex	Timber	Year
A. VIT only	0.14 (0.05)	2.88 (0.95)	-0.02 (0.04)	-1.66 (0.83)	-0.16 (0.67)	1.73 (0.69)
B. Combined, with group						
Hoof growth eq.	0.12 (0.02)	0.49 (0.31)	0.02 (0.02)	-0.06 (0.32)	0.42 (0.34)	0.50 (0.34)
Capture window	0.11 (0.02)	0.31 (0.69)	0.02 (0.02)	-0.09 (0.32)	0.44 (0.34)	0.44 (0.36)
C. Combined, w/out group						
Hoof growth eq.	0.13 (0.02)	0.37 (0.26)	0.03 (0.02)	-0.05 (0.32)	0.43 (0.34)	0.41 (0.33)
Capture window	0.12 (0.02)	0.52 (0.23)	0.03 (0.02)	-0.04 (0.31)	0.44 (0.34)	0.39 (0.35)
D. Opportunistic only						
Hoof growth eq.	0.10 (0.02)	0.34 (0.21)	0.04 (0.03)	0.17 (0.40)	0.30 (0.44)	0.19 (0.42)
Capture window	0.10 (0.02)	0.47 (0.29)	0.04 (0.03)	0.19 (0.40)	0.30 (0.43)	0.07 (0.45)
E. Simulated truncation						
Sim, -1 day	0.05 (0.04)	3.49 (1.39)	0.7 (0.07)	-1.58 (1.08)	1.05 (0.88)	0.33 (0.77)
Sim, -2 day	0.02 (0.04)	1.69 (1.43)	0.13 (0.09)	0.75 (1.58)	3.56 (1.72)	-0.05 (0.89)

Table 2.4. Comparison of AICc-Based Model Selection for Varying Levels of Left Truncation in Survival Data.

A–E indicate level of truncation, from least to greatest. Only models ranked within 2 AICc units of the best model within a set are shown

Model structure	Age	Mass
A. VIT only	0.14 (0.05)	2.88 (0.95)
B. Combined, with group		
Hoof growth eq.	0.12 (0.02)	0.49 (0.31)
Capture window	0.11 (0.02)	0.31 (0.69)
C. Combined, without group		
Hoof growth eq.	0.13 (0.02)	0.37 (0.26)
Capture window	0.12 (0.02)	0.52 (0.23)
D. Opportunistic only		
Hoof growth eq.	0.10 (0.02)	0.34 (0.21)
Capture window	0.10 (0.02)	0.47 (0.29)
E. Simulated truncation		
Sim, -1 day	0.05 (0.04)	3.49 (1.39)
Sim, -2 day	0.02 (0.04)	1.69 (1.43)

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CHAPTER 3. EFFECTS OF ENVIRONMENTAL AND INDIVIDUAL VARIABLES ON SITKA BLACK-TAILED DEER POPULATION DYNAMICS[2]

3.1. ABSTRACT

The pathways through which environmental variability affects population dynamics remain poorly understood, limiting both ecological inference and management actions. Here, I use matrix-based population models to examine the population response to environmental variability and individual traits. Using Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in Southeast Alaska as a study system, I modeled effects of inter-annual process variance of covariates on female survival, pregnancy rate, and fetal rate, as well as summer and winter fawn survival. To examine the influence of process variance on population dynamics, I a) perturbed vital rates and b) perturbed the covariates supported in top vital-rate models by observed process variances (i.e., retrospective analysis), then used the vital rates predicted from these models to perturb the matrix model. By comparing the baseline (mean) population growth rate ($\lambda = 1.08$) to the perturbed growth rates, I estimated the effect of vital rates and underlying predictive variables on population growth rate. Because deer population density and age distributions were not available during this study, these results apply only to population dynamics during the study, and should not be used quantitatively to predict future response of the population to environmental change. I found adult female survival was the most influential vital rate based on classic elasticity analysis (i.e., prospective analysis), however, elasticity analysis based on process variation (i.e., retrospective analysis) indicated that winter and summer fawn survival were most variable and thus most influential to variability in population growth. Summer fawn mortality was primarily determined by black bear predation, and was positively influenced by mass at birth and female gender. Winter fawn survival was determined by malnutrition in deep-snow winters, and was influenced by date of birth and snow depth, with late-born fawns

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[2] Gilbert SL, Hundertmark KJ, Lindberg MS, Person DK, Boyce MS (In prep). Elasticity of environmental and individual variables in Sitka black-tailed deer. Prepared for submission to the Journal of Animal Ecology.

at greater risk in deep-snow winters. Covariate elasticities indicated that total snowfall was the most important covariate, with an increase to 2 m of total snowfall (i.e., 2 SDs based on process variability) reducing fawn survival to zero, and population growth by 19% in the current year. Further, modeled declines in pregnancy rate in the following year reduced population growth by 11% in the following year. Integrating the effects of covariates on vital rates and population growth based on observed variability, as I do here, provides new insight into the environmental drivers of population processes.

3.2. INTRODUCTION

Drivers of animal population dynamics have long intrigued ecologists, yet linking changes in environmental conditions to population-level responses remains a central challenge (Forrester & Wittmer 2013; Jenouvrier et al. 2012; Ozgul et al. 2010). Environments are complex and many features vary within years and seasons, and spatially across landscapes. Thus, the effects of environmental variables on dynamics of populations can differ annually, seasonally, and spatially both in magnitude and direction. Moreover, those effects may manifest differently across life history stages within the population (Gaillard et al. 1998, Gaillard et al. 2013), and across population densities (Bowyer et al. 2014). Unfortunately, population responses to environmental drivers are rarely investigated across life history stages. Rather, inference regarding population responses to environmental change is frequently drawn from studies of a single important life history phase, typically the adult female. Important drivers of fitness for this life history phase are then assumed to also be the primary drivers of population dynamics. Yet even strong effects of predictive variables on life history phase may not matter in the context of population dynamics, if those vital rates are relatively unimportant in determining population growth (i.e., low elasticity) or the predictive variables do not vary through time or space (i.e., low contribution to variation in growth rate) or cannot be manipulated through management actions.

Advances in modeling have led to substantial progress in understanding the effects of environmental and individual variables on vital rates, such as survival (Blums et al. 2005; Monteith et al. 2013; Pollock et al. 1989; Tsai et al. 1999) and reproductive success (Delgiudice et al. 2007; Therrien et al. 2008; Tollefson et al. 2010). In parallel,

our understanding of how vital rates affect population dynamics in variable environments has also improved dramatically with the advent of stochastic and density-dependent population models (Grant & Benton 2000; Hunter et al. 2010), life table response experiments (LTREs; Caswell 2001; Caswell 2010) and life stage simulation analyses (LSAs; Mills & Lindberg 2002; Wisdom et al. 2000). Yet studies of variables affecting vital rates, and those focused on the effects of vital rates on population dynamics are rarely united (but see Aldridge & Boyce 2007 and Mason et al. 2014). Combining these approaches would be particularly useful in the study of large, long-lived animals such as ungulates, because environmental drivers primarily affect population growth through highly variable vital rates (e.g., juvenile survival), yet studies typically focus on low-variability, high elasticity rates such as adult survival (Gaillard et al. 1998; Gaillard et al. 2000).

In this study, I examine the response of Sitka black-tailed deer (*Odocoileus hemionus sitkensis)* vital rates and population dynamics to variables acting at scales of the environment and individual deer. Further, I scale up effects on individual fitness to examine their influence on population dynamics. Sitka black-tailed deer provide an excellent system for development of such a combined modeling approach. They are the primary herbivore in the coastal temperate rainforest of Southeast Alaska, and an important source of protein for subsistence hunters, wolves, and black bears. While winter is thought to limit deer populations in this system (Doerr et al. 2005; Farmer et al. 2006; Klein & Olson 1960; Person et al. 2009), predation can affect how quickly deer populations rebound from severe winters (Alaska Department of Fish and Game 2013; Lewis & Klein 1992). In addition, industrial-scale timber harvest creates even-aged seral stands with poor winter forage (Alaback 1982; Farmer & Kirchhoff 2007), reducing the resilience of deer populations to both severe winters and predation (Farmer et al. 2006; Person et al. 2009). Previous studies have focused almost exclusively on adult female survival (Farmer et al. 2006; Person et al. 2009), without studying reproduction and subsequent fawn survival. This is a troubling gap in knowledge, as juvenile survival drives most observed variation in population growth rates for ungulates (Gaillard et al. 1998; Gaillard et al. 2000).

I developed hypotheses regarding the environmental and individual-level drivers of fitness (Table 3.1) for each adult vital rate (pregnancy, fetal rate, and annual survival), and fawn vital rate (summer and winter survival). I expected that adult female survival would have the largest relative influence on population dynamics based on classic (prospective) elasticity analysis, but that process variation in juvenile survival should be the highest of all the vital rates, and have the greatest influence on population dynamics when perturbations are based on process variance. As a result, predictive variables associated with fawn survival should also be most influential when changed based on process variation.

3.3. METHODS

3.3.1. Study Area

Our study was conducted on central Prince of Wales Island, the largest among the many islands of the Alexander Archipelago of Southeast Alaska (Figure 3.1). The study area is typical of the coastal temperate rainforest of the region, although with gentler topography, milder winter conditions, and more productive forest than many other islands in Southeast Alaska. Nevertheless, topography can be quite rugged due to the limestone and granite bedrock underlying much of the landscape, ranging from 0 to 1200 meters above sea level. Due to moderate annual temperature variation, plentiful precipitation (> 300 cm per year) falls as rain in summer, and as both rain and snow in winter, although snowpack sometimes persisting at depths >1m for weeks at a time even at relatively low elevations. Natural habitat types are widely varied, including old-growth forest, numerous lakes, rivers and estuaries, alpine and subalpine vegetation above ~400 m, and muskeg heaths (Alaback & Saunders 2013).

The favorable environmental conditions relative to the region as a whole have long supported abundant populations of key species such as Sitka black-tailed deer, black bears, wolves, eagles, and salmon that comprise a predator-prey system that also includes human hunters. In addition, central Prince of Wales continues to be the focus of industrial timber harvest in the Tongass National Forest, including in the study area (U.S. Forest Service 2008), resulting in disproportionate harvest of productive old-growth forests (Albert & Schoen 2013). Timber harvest produces even-aged stands that gradually gain

canopy cover and correspondingly lose forage biomass through successional stages, regaining old-growth properties after more than 200 years (Alaback 1982; Alaback & Saunders 2013).

3.3.2. Deer Capture and Monitoring

All animal capture and handling was carried out in accordance with the University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC #136040-14) regulations. A total of 63 adult female deer (age 2 years and older) were captured from mid April through mid May of each year, from 2010-2012, as well as from July 5-25th during 2010 (n = 20 in 2010, n = 21 in 2011, and n = 22 in 2012). I did not capture yearling (age 1 year) animals during this study, but Farmer et al. (2006) and Person (2009) studied deer in adjacent and overlapping study areas, and found no difference in survival or causes of mortality between adult and yearling females. At capture, morphological measurements (i.e., heart girth, body length, hind foot length) were measured, blood collected, and body condition and pregnancy assessed using a portable ultrasound machine (Sonosite Titan, Sonosite, Bothel, WA). I estimated female body mass based on measured hearth girth (Parker 1987), and ingesta-free body fat based on body mass and MAX rumpfat measurements from ultrasonography (Cook et al. 2010). Adult females were classified as 2, 3, and 4 + years old based on tooth wear (Hamlin et al. 2000), but I combined 3 and 4+ year olds into a single, adult age class. Each deer was fitted with a GPS radiocollar, and monitored weekly in summer (April-August 1) and every 2 weeks during the remainder of the year.

If pregnant (n = 53), adult females were fitted with vaginal implant transmitters (VITs; Advanced Telemetry Systems, Isanti, MN), allowing us to monitor females daily prior to parturition, locate the birth site, and capture neonates (Carstensen et al. 2003; Gilbert et al. 2014). Two adult females had vaginal canals too narrow to accommodate the vaginoscope used in VIT implantation; of the adult females fitted with VITs (n = 49), I successfully captured neonates from 65% (n = 32). Neonates were gently restrained with eyes covered to reduce agitation. I determined weight, gender, and morphological measurements, and fitted fawns with VHF (all years) and GPS (n = 30, 2012) collars. Fawns were subsequently monitored 1-2 times per day from birth until August 1, then

every 2 weeks until 1 year of age. Mortality was signaled after 5 hours of collar inactivity, and mortality events were investigated promptly upon discovery to determine cause of death.

In total, 45 neonatal deer fawns were captured at birth, whereas an additional 109 neonates were captured opportunistically along roads and trails and when spotted in meadows and clearcuts. However, because mortality is highly age-dependent for neonatal deer, resulting in more vulnerable animals dying at birth or shortly thereafter, I excluded opportunistically captured neonates from analysis of summer survival to avoid left truncation of data (Gilbert et al. 2014). In addition, I lacked information on maternal predictive variables such as maternal age, body mass, and body fat for opportunistically captured fawns. However, because daily survival rates and thus left-truncation bias converge in the system at approximately 30 days of age, I included opportunistically captured fawns in winter fawn survival estimates, increasing the winter sample size to 81 individuals.

3.3.3. Effects of Predictive Variables on Vital Rates

I estimated vital rates, including mean rates across the 3 years of the study and for each year. Vital rates estimated were pregnancy and fetal rates, summer and winter survival rates for fawns, and annual survival rates for adults. Pregnancy and fetal rate were modeled using generalized linear models in program R (R Core Development Team 2014) and were treated as binomial and Poisson responses, respectively (Caswell 2001; Morris & Doak 2002).

For adults, I expected all vital rates to respond positively to age, body mass, and body fat (Delgiudice et al. 2006; Delgiudice et al. 2007; Mueller & Sadleier 1979; Johnstone-Yellin et al. 2009), and negatively to timber harvest and winter severity, with potential lagged negative effects of winter in following years (Fryxell et al. 1991; Robinette et al. 1957; Verme 1977). Although I hypothesized that female body fat should affect pregnancy and fetal rates, I did not consider adult female body fat as a covariate for pregnancy or fetal rate because body condition was measured in early spring, after pregnancy and fetal rate had already been determined, rather than in autumn. Only 6 adult female deer died among the 63 monitored over 3 years. This low number of events

limited the number of parameters that could be examined simultaneously. Models with fewer than 10 events per variable can produce biased model estimates and Type I predictor selection error, although recently there has been argument that this rule can be relaxed (Vittinghoff & McCulloch 2006). As a result, I only examined the univariate effects of age, mass, body fat, and timber harvest regime on survival.

Responses of fawn and adult female survival to environmental and individual predictive variables were modeled using known-fates survival models, implemented in the RMark package in program R (Laake 2013). In Southeast Alaska, most fawn mortality during summer is caused by black bear predation (Gilbert et al. 2014), whereas most winter mortality is caused by wolf predation and malnutrition (Person et al. 2009). Because the level of compensation between predation and other causes of mortality (Monteith et al. 2013) is not known for this system, I considered predictive variables of survival that were linked to nutrition as well as those that were linked to behavior and habitat (Table 3.1).

I considered fawn survival in separate summer and winter periods, because vulnerability to predation, sources of mortality, and therefore effects of predictive variables change from birth through the first year of life. The neonatal period, when fawns are typically most vulnerable to predation (Whittaker & Lindzey 1999; Pojar & Bowden 2004), began at birth and continued to 90 days of age, by which age most summer fawn mortality had occurred (Figure 3.3). During this period, survival was modeled in weekly intervals, with a linear effect of time as survival increases markedly with fawn age (Gilbert et al. 2014). The fall and winter period, henceforth referred to as the over-winter period, extended from 91 to 365 days of age, and survival was considered in 2-week intervals, without an effect of time.

I hypothesized that fawn survival should be influenced by maternal quality, and thus maternal age, mass, and body fat should increase fawn survival in both summer and winter. Likewise, mass at birth should increases summer survival by reducing predation risk (Lomas & Bender 2007; Johnstone-Yellin et al. 2009; Hurley et al. 2011), and increase winter survival if early mass deficits persist (Loison et al. 1999; Whiting et al. 2010). Similarly, litter size should reduce summer survival through decreased maternal investment and/or increased vulnerability to predation (Johnstone-Yellin et al. 2009; Van

Vuren et al. 2013). In addition, birth synchrony should increase summer survival through reduced predation risk (but could have a negative effect instead; Sinclair et al. 2000) and enhanced overlap with peak plant nutrition (Langvatn et al. 2004; Parker et al. 2009). Females may survive at higher rates than males due to less conspicuous behavior and slower growth rates (Jackson et al. 1972; Loison et al. 1999). In contrast, late-born fawns should be less vulnerable to bear predation as bears focus on salmon in late summer (Hilderbrand et al. 2004), but more vulnerable to winter starvation due to small body size (Loison et al. 1999; Whiting et al. 2010). Finally, timber harvest could reduce summer fawn survival by concentrating both deer and bears in young productive clearcuts; and winter severity and timber harvest could interactively reduce winter fawn survival, as young clearcuts with deep snow provide poor forage, whereas older clearcuts support little plant biomass (Alaback 1982; Farmer & Kirchhoff 2007; Hanley 2005).

Nutritional condition of fawns prior to winter was not measured because fawns were not re-captured. Therefore, with respect to winter survival of fawns, I included an effect of mass at birth, and back-calculated mass at birth for opportunistically captured fawns by assuming a universal age of 5 days at capture. Many studies determine age of opportunistically captured fawns based on new hoof growth (Haskell et al. 2007; Sams et al. 1996), however existing hoof growth equations were recently demonstrated to be inaccurate for mule deer (Grovenburg et al. 2014). Instead, I empirically generated a potential capture-age window by re-capturing fawns caught at birth up until the age at which they could no longer be recaptured (11 days), and assigned the median of this period (5 days) as the age at capture (Johnson et al. 2004; Gilbert et al. 2014).

To identify top and competing models for inference, I began with a global covariate model for each vital rate, based on hypothesized ecological relationships described previously. I reduced the global model for each vital rate into subset models with a maximum of 3 predictive variables per model due to the limited sample sizes and numbers of mortality events. Variables that were highly correlated with each other ($|r| > 0.6$) were not included in the same sub-models to prevent coefficient bias. For each vital rate, a competitive model set was formed of models with AICc scores that differed ≤ 2 from the model with the lowest AICc score. I then discarded models with uninformative variables from the competing model set, defined as models where the model was simply a

hierarchical expansion of the top-ranked model with no reduction in log likelihood (Arnold 2010; Burnham & Anderson 2002).

3.3.4. Estimation of Process Variance in Vital Rates and Predictive Variables

Temporal process variation in the vital rates was estimated by fitting a model without covariates for each vital rate, but with a group (strata) effect of year, which I then used to estimate the mean and standard error for each vital rate in each year (i.e., raw variation in vital rates across years; Morris & Doak 2002; White 2000). Then, I used the approach proposed by White (2000) to partition process from sampling variance, implemented in program R. The resulting mean vital rates, with variance partitioned into sampling and process components, were used in subsequent matrices. Temporal process variance in predictive variables of vital rates was estimated using different approaches for environmental and individual variables. Variation in individual variables between years was assumed to contain both process and sampling variance, as estimates depended on the animals sampled. However, some environmental variables, i.e., snow depth recorded at Annette Island weather station, were presumed to be purely the result of process variance, whereas others, i.e., timber-harvest regime of the watershed, were presumed to be purely the result of sampling variance. For individual variables, I estimated the inter-annual process variance by constructing generalized linear models of each covariate with an effect of year in the model, then used the maximization approach of White (2000) to partition process from sampling variance, as before. For timber-harvest regime of watershed, which I recorded as a binary factor, I assumed that there was no process variance between years in the study, as little new timber harvest occurred during this short period of time at the scale of watersheds. To quantify winter severity, I examined variation in total annual snowfall at Annette Island from 1995-2014 (Figure 3.2) as a measure of inter-annual variability, and assumed that all observed variance was process variance.

3.3.5. Effects of Vital Rates and Predictive Variables on Population Dynamics

To determine the effects of each covariate on population dynamics, I used the fitted relationships from the top model for each vital rate identified based on AICc score

(Table 3.2) to generate predicted vital rates while perturbing predictive variables by two times the standard deviation of that covariate (calculated as the square root of process variance). If a variable occurred in more than one vital rate model, I perturbed all vital rates affected by that variable simultaneously so that the combined effects of each variable were incorporated into covariate elasticity calculations. For each variable perturbation, I then used the predicted vital rate responses as inputs into a matrix-based population model. The post-birthpulse model structure included 3 age classes (Figure 3.3, fawns, yearlings, and adults, although the transition probability for the first age class was subdivided into summer and winter survival, as discussed previously. The matrix structure was specified as follows:

$$\begin{bmatrix} N_{f(t+1)} \\ N_{y(t+1)} \\ N_{a(t+1)} \end{bmatrix} = \begin{bmatrix} 0 & P_y * F_y & P_a * F_a \\ S_{f(s)} * S_{f(w)} & 0 & 0 \\ 0 & S_y & S_a \end{bmatrix} \begin{bmatrix} N_{f(t)} \\ N_{y(t)} \\ N_{a(t)} \end{bmatrix} \qquad (1)$$

Where N_j is the number of individuals in age class j at time t, $N_{j(t+1)}$ is the number of individuals in age class j at time $t+1$, S_j is the survival probability of age class j, and P_j and F_j are the pregnancy rate and fecundity (as females per female) respectively, of an individual of age class j. Because I did not capture any yearling individuals, I assumed that survival of yearlings was equal to that of adult females, as found in a previous study adjacent to the study area (Farmer et al. 2006). Pregnancy and fecundity of yearlings was measured during the course of this study, despite the fact that no yearlings were captured, because animals that were captured in the spring and aged as 2 years old were in fact primiparous yearlings (Figure 3.3).

For comparison with the perturbed matrix for each variable, I constructed a baseline matrix, with mean vital rates calculated from the top-ranked models and predictive variables held at mean values. I then calculated the covariate elasticity of each vital rate as the percent difference in the dominant eigenvalues (i.e., growth rates, λ) of the two matrices:

$$Ec = \frac{\lambda_{pert} - \lambda_{base}}{\lambda_{base}} \qquad (2)$$

Where *Ec* is the covariate elasticity, $\lambda_{base}$is the dominant eigenvalue of the baseline matrix, and λ_{pert} is the dominant eigenvalue of the perturbed matrix. I examine the effects of a positive versus negative perturbation to each covariate, resulting in positive and negative changes to λ_{pert} depending on the sign of the covariate coefficient. To determine the potential effects of vital rates on population dynamics (i.e., prospective analysis) I calculated elasticities of the vital rates. To determine retrospectively which vital rates contributed to observed inter-annual variability in growth rate, I conducted life table response experiments (LTRE; Caswell 2001; Morris & Doak 2002), using the "popbio" package (Stubben et al. 2012) in program R. Elasticities of vital rates were calculated from the baseline matrix, λ_{base} and are interpreted as the prospective potential of a vital rate to affect future growth rate. Contributions of vital rates to variation in growth rate (i.e, LTRE; Caswell 2001) were based on sensitivity analysis of vital rates within the mean matrix between a treatment matrix and the baseline matrix. In this case, the vital rates for the "treatment" matrix were simply baseline vital rates reduced by 2 standard deviations, with standard deviations calculated from estimated process variance for each vital rate (Table 3.2). If a vital rate had zero estimated process variance, it was not perturbed. Because all vital rates with observed process variance were reduced simultaneously to produce the treatment matrix, covariance between these vital rates was assumed. In this case, vital rates perturbed included only pregnancy rate and summer and winter fawn survival, not fetal rate or adult survival.

It is worth noting that gender was a covariate of fawn survival, yet I used a single-gender, all-females model for prediction of the effects of predictive variables, including gender. Perturbing the frequency of gender affects fawn survival, but is equivalent to changing the gender ratio (i.e., number of female fawns per female at birth). However, as I found no process variance (<0.001) in gender ratio between the years of the study, I did not perturb gender.

3.4. RESULTS

I captured 63 adult female deer from 2010-2012, 53 in spring prior to parturition, and 10 in mid to late June. Among spring-caught females, 47 were pregnant, yielding an

average pregnancy rate of 0.91 (total var = 0.03, process var = 0.009). Across years, females had pregnancy rates of 1.0 (*SE*=0) in 2010, 0.95 (*SE*=0.05) in 2011, and 0.77 (*SE*=0.09) in 2012 (Figure 3.3. Of the 44 adults fitted with VITs, I was able to successfully capture 45 fawns from 32 (73% of) individual females. The average fertility rate for pregnant females was 1.45 fawns per female (total var = 0.07, process var <0.001), implying a rate of 0.72 female fawns per female if a 1:1 gender ratio is assumed. The rate of female fawns per female measured from the captured fawns was 0.625 female fawns per female (*SE* = 0.10), with an upper 95% confidence interval of 0.82; as a result I accepted the 1:1 gender ratio assumption. Among years, the fertility rate was 1.67 fawns per female (*SE* = 0.43) in 2010, 1.36 (*SE* = 0.35) in 2011, and 1.33 (*SE* = 0.33) in 2012.

As previously discussed, annual adult survival was high and showed little process variance, averaging 0.90 (total var = 0.005, process var < 0.001) for the study period, and varying little between years (*M* = 0.89, *SE* = 0.07 in 2010; *M* = 0.85, *SE* = 0.08 in 2011; and *M* = 0.95, *SE* = 0.04 in 2012; Figure 3.3. The largest source of mortality (n = 3, *M* = 0.05, *SE* = 0.03) was from hunting, followed by malnutrition (*n* = 2, *M* = 0.03, *SE* = 0.02) and black bear predation (*n* = 1, *M* = 0.02, *SE* = 0.02). Wolf mortality was not recorded for adult deer monitored during this study, despite wolf predation acting as a major source of mortality for deer monitored in the same study area 10 years previously (Person et al. 2009). Wolves are currently at low numbers and restricted distributions due to high trapping pressure (Alaska Department of Fish and Game 2014).

Fawn survival was lowest during the summer, due primarily to predation by black bears, and highly variable between years, in part due to process variance. Mean survival in summer was 0.41 (total var = 0.06, process var = 0.01), and annual summer survival rates were 0.47 in 2010 (*SE* = 0.13), 0.23 in 2011 (*SE* = 0.11) and 0.54 in 2012 (*SE* = 0.13; Figure 3.3. Across all years, mortality rates were 0.46 (*n* = 21, *SE*= 0.08) due to black bear predation, and 0.11 (*n* = 6, *SE* = 0.05) due to other causes. Other causes of mortality included unknown predation (*n* = 1), eagle predation (*n* = 1), drowning (*n* = 1), and premature birth (*n* = 3). As before, maternal mass and age were correlated (*r* = 0.56), and were not included in the same models. In addition, synchrony of births was lower in timber harvested watersheds (*p* = 0.015), although the two variables were only moderately correlated (*r* = 0.36).

During the winter months, fawn survival was determined primarily by malnutrition-caused mortality, which occurred only during the winter of 2011 (Figure 3.3. Across the three years of the study, the average winter survival rate was 0.73 (total var = 0.17, process var = 0.08), due to a mortality rate of 0.21 (n = 16, SE = 0.05) from malnutrition, 0.03 (n = 2, SE = 0.02) from wolf predation, 0.02 (n = 1, SE = 0.02) from bear predation (in late September), and 0.03 (n = 2, SE = 0.02) due to other causes (n = 1 car collision, n = 1 illegal hunting). Between years, winter survival rates were high in 2010 (M = 0.84, SE = 0.07) and 2012 (M = 0.96, SE = 0.04), and quite low in 2011 (M=0.40, SE=0.09).

3.4.1. Effects of Predictive Variables on Vital Rates

Variables that affected probability of pregnancy were the severity of the preceding winter as measured by total snowfall (winter(t-1)), adult female age, and timber harvest of watershed, with the best-supported model including winter(t-1) and timber harvest (Table 3.3). Adult female age had a positive effect on probability of pregnancy, as did occupancy of a timber-harvested watershed, whereas a winter with greater total snowfall reduced the probability of pregnancy in the following spring. Fetal rate was not strongly affected by any predictive variables; the null model was top-ranked although a positive effect of female age ($\Delta AICc$ = 1.24; Table 3.2) and female mass ($\Delta AICc$ = 1.83) also received support. Female age and female mass were positively correlated for pregnant females (r = 0.60, $p < 0.01$) and for females where fawns were captured (r = 0.57, $p < 0.01$), and as a result female age and female mass were not simultaneously included as variables in any vital rate models. Based on the univariate analysis of predictive variables of female survival, there was support for negative effects of female mass and age on survival (i.e., younger, lighter-weight females survived with higher probability; Table 3.3).

Summer fawn survival, from birth through 90 days of age, was affected by both gender and birth mass. In the top-ranked survival model, female fawns had a higher survival probability than male fawns, as did fawns that weighed more at birth (Table 3.3). Other competitive models included a negative effect of birth synchrony on survival, indicating that fawns born more synchronously survived at lower rates, and a positive

effect of winter severity in the previous year. Although there were no strongly correlated predictive variables, there was a statistical relationship between timber harvest of watershed and birth synchrony, with more asynchronous births in timber harvested watersheds ($r = 0.34, p = 0.015$).

Winter fawn survival, from 91 through 365 days of age, was strongly affected by winter severity and birthdate. The top-ranked model supported negative effects of winter severity and birthdate, indicating that late-born fawns are at greater risk of mortality, as are fawns during high-snowfall winters. In addition, a competing model supported an interactive, negative effect of winter severity and birthdate, indicating lower survival during severe winters and for late-born fawns (Table 3.3).

3.4.2. Effects of Vital Rates and Predictive Variables on Population Dynamics

Analysis of the baseline population model indicated that the average population growth rate for the study period was distinctly positive, with $\lambda = 1.08$, despite the harsh winter of 2011, with a predicted stable stage distribution of 38% fawns, 11% yearlings, and 51% adult females in the population at equilibrium. Annual estimates of deterministic population growth rates were 1.17 in 2010, 0.92 in 2011, and 1.18 in 2012. Prospectively, the most influential vital rate based on elasticity values (Table 3.4; Figure 3.3) was adult female survival, followed by summer and winter fawn survival, survival of yearlings, fertility of adults and yearling, and pregnancy of adults and yearlings. However, retrospective analysis revealed that when vital rates were perturbed based on process variation, relatively high levels of process variation resulted in winter fawn survival contributing most to variation in growth rate, followed closely by summer fawn survival, then by adult and yearling pregnancy rate, with other vital rates contributing much less due to almost no process variation (Table 3.4; Figure 3.3).

Retrospectively, covariate elasticity (*Ec*) analysis revealed that winter severity, as measured by total snowfall, had the largest effect on population growth rates (Table 3.4; Figures 3.4, 3.5) with an increase in winter snowfall from the mean observed during the study (0.71 m) by 2 SD of the process variance observed over 20 years (1.29 m) resulting in a 19% decrease in growth rate due to reduced survival of fawns in winter, and an 11% decrease in year $t + 1$ due to reduced pregnancy rates. However, because survival and

pregnancy rates could not go above 1, an equal decrease in winter snowfall resulted in much less of an increase in growth rate during the current year (2.9%) and following year (0.7%; Table 3.4; Figure 3.4). Fawn mass was another influential covariate (Figure 3.5), with a reduction in fawn mass from the mean (2.63 kg) by 2 SD (0.23 kg) resulted in a 6.7% decrease in growth rate, and an equal increase in mass resulting in a 6.2% increase in growth rate. Timber harvest was assumed to have no process variance within the study, and so was not perturbed. Gender had very low process variance, and as a result, had almost no influence on growth rate. Birthdate also had low process variance, and was perturbed from a mean value of 17.60 days (after May 24th, first recorded birth), by 2 SD (1 day), resulting in a 0.2% increase or decrease to growth rate.

3.5. DISCUSSION

Although many of the hypotheses regarding the drivers of deer vital rates and population dynamics were supported, there were also some intriguing and unexpected outcomes from the analyses. For adult females, probability of pregnancy and fetal rate were higher for older females, as predicted, and adult female mass positively affected fetal rate. These results agree with life-history theory, in which older and larger females typically produce more offspring at more frequent intervals (Hamel et al. 2009; Lindberg et al. 2013). Although reproductive senescence is thought to occur in Sitka black-tailed deer (Johnson 1987), the proportion of senescent individuals in the adult population is likely low, as evidenced by the positive effect of age on reproduction. Interestingly, there was a mild positive effect of timber harvest on probability of pregnancy; in addition, synchrony of births was negatively affected by timber harvest, indicating that some feature of these altered watersheds is affecting deer conception probability and timing and suggesting the need for further inquiry. Based on the univariate analysis of predictive variables of adult survival, female mass negatively affected survival of adult females, likely because hunters selected for larger individuals. Hunting was the primary cause of death for adult females, and larger animals are typically preferred by hunters (Brinkman et al. 2009; Milner et al. 2007). Thus, large body mass could decrease adult female risk from natural causes, as has been documented in other systems, but increase risk from human hunting.

Summer fawn survival was the lowest survival rate, with more than half of all fawns dying before three months of age on average (Table 3.1), primarily from bear predation. Summer fawn mortality risk and bear mortality risk were negatively affected by birth mass and fawn gender, with larger fawns and female fawns surviving with higher probability. Behavioral differences between male and female fawns have been observed, with male fawns engaging in more conspicuous behaviors (i.e., active more of the time; Jackson et al. 1972), likely increasing detection probability by bears. In addition, synchrony of birth decreased summer survival, possibly because bears actively search for fawns only during the peak of births. Surprisingly, the severity of the previous winter positively affected summer fawn survival, possibly because low-quality adult females were selectively removed from the population, along with their unborn offspring, or lost fetuses prematurely and did not give birth. Bear predation risk appears to be linked to nutrition of fawns, given the strong effect of fawn mass at birth on summer survival, and thus is likely partially compensatory. However, maternal body fat did not predict fawn survival, suggesting that perhaps females conserve body fat at the expense of fawn mass at birth (i.e., the "selfish" female hypothesis, Festa-Bianchet & Jorgenson 1998, Parker et al. 2009, Therrien et al. 2008).

Overwinter fawn mortality was almost entirely driven by malnutrition in the single harsh winter, with very high fawn survival during the other years. Negative effects of later birthdate, winter severity, and the interaction between these two terms were supported, indicating that late-born fawns, which enter winter at smaller mass and with fewer body reserves, are at correspondingly greater risk of malnutrition. Intriguingly, I recorded no effect of birth mass, demonstrating that fawns were able to recover from early deficits in body mass. Although there was no support for an effect of timber harvest on winter survival, the connection between timber harvest and birth asynchrony indicates that timber harvest can affect birth timing, and merits further investigation given the importance of birthdate for winter survival.

Although timber harvest did have a negative effect on fawn and adult female survival based on coefficient values in models in which it occurred, the standard errors of the term were high, leading to the exclusion of the term from final models. Timber harvest regime of watershed is a very coarse variable, homogenizing variation in seral

stage and corresponding nutrition within deer home ranges. In addition, deer select habitat from within the home range (Johnson 1980), and may be able to increase access to nutrition through selection (Parker 2003). Age and configuration of harvested stands, as well as quality and size of remaining old-growth forest patches, is likely important in determining winter survival. A detailed analysis of seasonal habitat selection and survival consequences that includes stand-level variation in seral stage, biomass, and snow depth is an important next step.

The effects of predictive variables on population growth indicated that winter severity, as measured by total snowfall, had the greatest negative impact on growth rate given current population conditions. Reductions to winter fawn survival were dramatic as total snowfall increased, and a winter with a total snowfall of 2m (i.e., 2 *SD* increase), resulted in fawn survival probability of <0.001, and a corresponding growth rate of 0.91. Population growth transitioned from positive to negative (i.e., growth rate =1.00) when total snowfall was 1.27 m and fawn winter survival was 0.35 (*SE* = 0.09). In addition, the modeled decrease in pregnancy rate in the following spring to a probability of pregnancy of 0.36 (*SE* = 0.34) caused a decrease to the following year's growth rate of 11%. Total annual snowfall greater than 2 m (at Annette Island, station of record for this study) occurred twice in the last 20 years (1998 and 2008), whereas total annual snowfall greater than 1.27 m occurred 6 times (Figure 3.2). However, the negative effects of winter documented here are the result of only 3 years of study, which were by no means as extreme as previously documented severe winters (Brinkman et al. 2011). In extremely severe winters, adult female survival can be greatly reduced (Alaska Department of Fish and Game 2013), whereas I documented only 2 deaths of adult females from malnutrition during the severe winter in the study, with no statistical effect on adult female survival. In addition, winter severity could interact with deer density relative to carrying capacity to influence survival and growth rate response (Bowyer et al. 2014), which I was not able to measure during the course of this study. Therefore it is likely that the effects of severe winters on population growth can be much greater than documented here, due to reduced adult female survival, or due to increased mortality of multiple age classes at high population density. In general, deer populations are density-dependent, although we do not include density in our population models. Therefore, we stress that our results should

be interpreted qualitatively, but not quantitatively, to better understand deer in other areas in Southeast Alaska or during other time periods in the study area.

In addition, it is important to note that although wolves killed 7% of adult and yearling females and 10% of fawns annually in the study area during the late 1990's (Alaska Department of Fish and Game unpublished data, Person et al. 2009), I observed no predation by wolves on adults. Moreover, few fawns were killed by wolves and only during the first year and in one of six watersheds. The wolf population on Prince of Wales Island has historically been among the densest in the state of Alaska (Person et al. 1996), but was greatly reduced due to human trapping and hunting (Alaska Department of Fish and Game 2014; Person & Russell 2008). Thus, an important regime shift has likely occurred in the study area, although a more detailed analysis is necessary to clarify the extent and impact of this shift.

Simply documenting that a covariate affects survival or reproduction is not enough to infer that it is important to population dynamics. This approach, in which multivariate models of vital rates are fitted and used to produce elasticities of predictive variables in a population matrix, provides one potential solution to bridging this inference gap. Here, I find that although adult female survival is highly influential in determining population growth in theory, it was neither highly variable nor highly responsive to environmental drivers during our study, nor does it contribute substantially to variability in population growth rate. This result conforms to other studies of ungulate population dynamics (Gaillard et al. 1998; Gaillard et al. 2000). In contrast, juvenile survival is strongly influenced by environmental and individual predictive variables, primarily by mass at birth and thus presumably nutrition during summer, and winter severity during the winter. Thus, variation in environmental predictive variables can influence population growth rate (given current population density and age distribution) most strongly through changes in fawn survival rather than adult survival. However, when an extreme event (i.e., very deep, persistent snow in winter) does reduce adult survival, the same event is likely to reduce juvenile survival and pregnancy rates much more, resulting in a compounded negative impact to population growth rate.

I found population dynamics in this system to be strongly driven by winter severity. Although I were unable to estimate the full demographic impact of extreme

winter weather events in this study, because such an extreme event did not occur during the three years of this work, I conclude through modeling efforts that such events would likely have large negative effects on deer populations in Southeast Alaska. Given projections for increased stochasticity and severity of weather under future climate change scenarios, such compounding, multi-vital-rate effects of environmental drivers may become increasingly influential for ungulate populations in many high-latitude systems. In this ecosystem, average winter snowfall is projected to decrease, whereas severity of stochastically occurring major storms may increase (Shanley et al. 2015), potentially leading to greater swings in deer population size as series of mild winters lead to high population densities, which then experience density-dependent negative impacts of occasional severe winters. Although survival of adult female ungulates is canalized against environmental variation (Gaillard & Yoccoz 2003), extreme events can overwhelm the resilience of this key vital rate (Brinkman et al. 2011), causing large demographic impacts through joint reductions of adult and juvenile survival. Understanding and predicting the effects of increased frequency of extreme events, and the interactive role that other environmental drivers such an anthropogenic habitat change could play in determining population response, is therefore an emerging challenge for population ecology and management.

3.6. ACKNOWLEDGEMENTS

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3.7. FIGURES

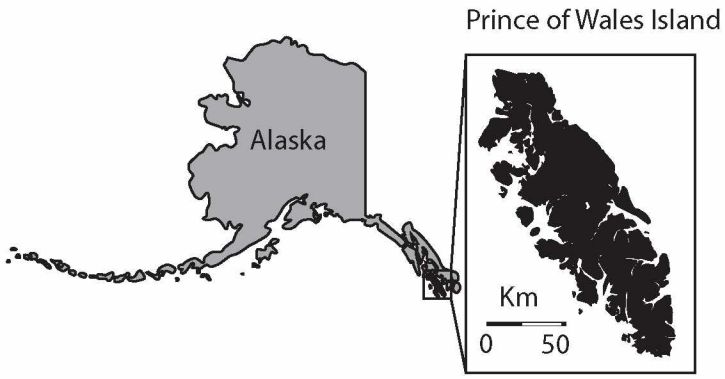

Figure 3.1. Study Area Map

The study area, located in the central portion of Prince of Wales Island in Southeast Alaska within the Tongass National Forest.

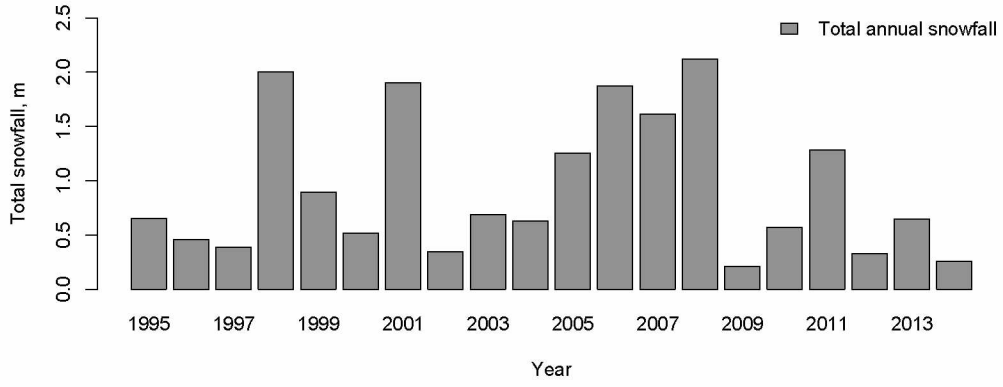

Figure 3.2. Twenty-Year Record of Total Annual Snowfall

Total annual snowfall recorded at Annette Island, adjacent to Prince of Wales Island and the closest long-term weather station to the study area in Southeast Alaska.

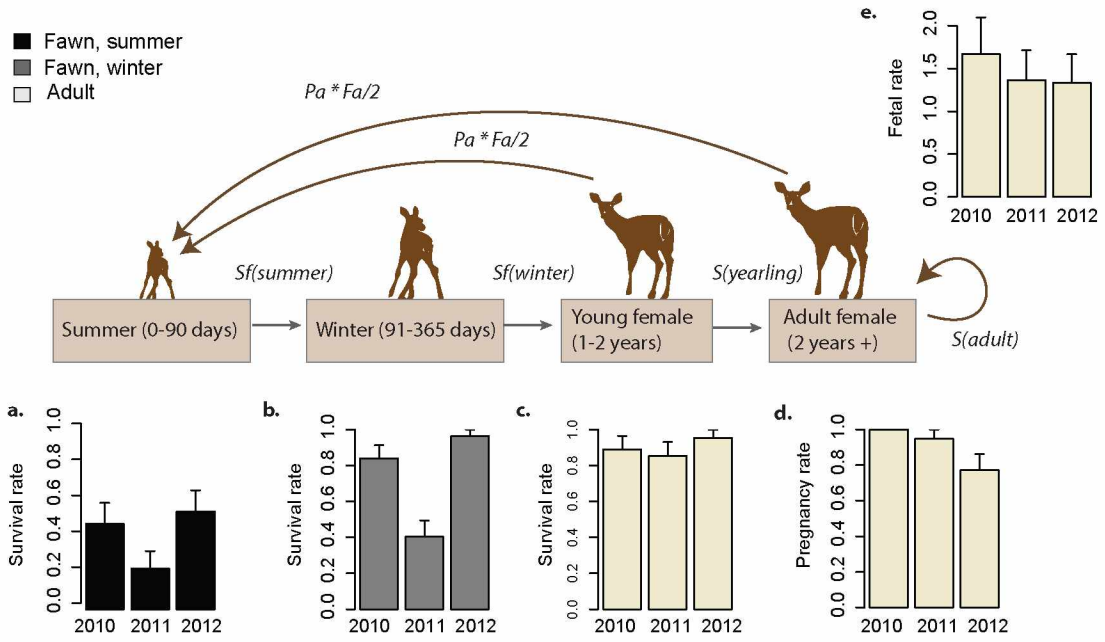

Figure 3.3. Life Cycle and Variability of Vital Rates for Deer

Inter-annual variability in vital rates, with standard error bars, is shown for 2010-2012, comprised of a) summer survival rate of fawns, b) winter survival rate of fawns, c) annual survival rate of adult females, d) pregnancy rate of adult and yearling females, and e) fetal rate of adult and yearling females.

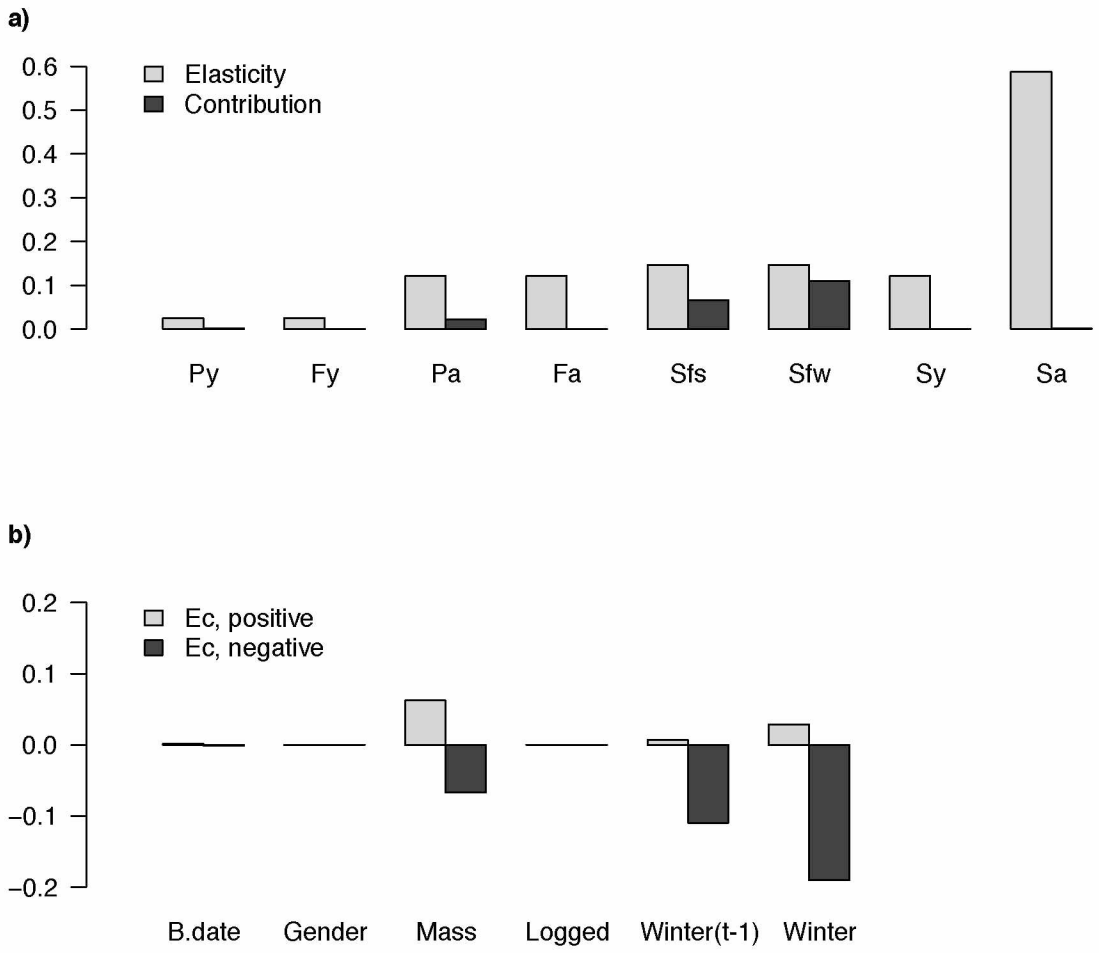

Figure 3.4. Prospective and Retrospective Effects of Vital Rates on Growth Rate. Prospective (elasticity) and retrospective (contribution) effects of vital rates, and elasticity of predictive variables for Sitka black-tailed deer. **a)** elasticity and contribution to inter-annual variability of growth rate for vital rates, where *P* denotes pregnancy, *Fy* and *Fa* denoted fertility (females per fawn) of yearling and adult females, and *Sf(s)*, *Sf(w)*, *Sy*, and *Sa* denote survival of age classes fawn (days 1-90), fawn (days 91-365), yearling, and adult females; and **b)** elasticity of predictive variables (*Ec*) from top-ranked models of vital rates, based on perturbation of covariate values by 2 times the process SD in a direction that positively (light grey bars, Ec_p) or negatively (dark grey bars, Ec_n) affected growth rates.

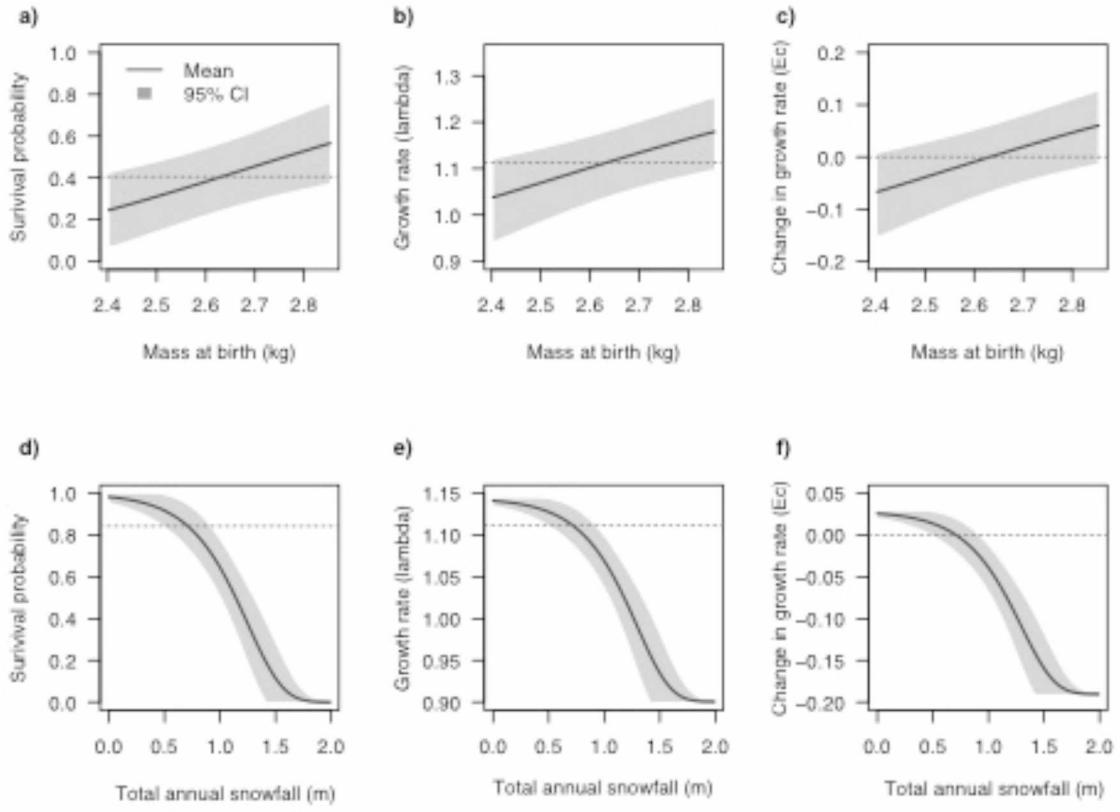

Figure 3.5. Effects of Predictive Variables on Vital Rates, and on Growth Rate, for Deer The effects of predictive variables on survival probability and growth rates, with corresponding covariate elasticities, shown with 95% CIs. Range of perturbation was by 2 standard deviations from the study mean, calculated from process variation of the predictive variables. The effect of a) fawn birth mass on summer survival on b) population growth rate, resulting in c) covariate elasticity for mass. The effect of d) total snowfall in witner, on d) population growth rate, resulting in e) covariate elasticity for total winter snowfall in year t, shown with mean and perturbed values of sever winter frequency.

3.8. TABLES

Table 3.1. Hypothesized Effects of Predictive Variables on Vital Rates of Deer

Plus (+) signs indicate a hypothesized positive effect on each vital rate, while negative signs (–) indicate a hypothesized negative effect on that vital rate.

	Vital Rate Response				
Variable	**Pregnancy**	**Fetal rate**	**Fawn S(t), summer**	**Fawn S(t), winter**	**Adult S(t)**
Female age	+	+	+	+	+
Female mass (spring)	+	+	+	+	+
Female fat (spring)		+	+		+
Fawn birth mass			+	+	
Fawn birth date			+	–	
Fawn birth synchrony			+		
Litter size			–		
Sex (female)			+	+	
Winter severity (t)				–	–
Winter severity (t-1)	–	–	–	–	–
Winter(t)*Birthdate				–	
Timber harvest	–	–	–	–	–

Table 3.2. Estimates of Vital Rates for Sitka Black-Tailed Deer

Mean estimates for 2010-2012 are shown as means with total variance (total σ^2), process variance (process σ^2), and sample size (N) .

Vital Rate	**Estimate**	***Total* σ^2**	***Process* σ^2**	***N***
Pregnancy Rate	0.91	0.03	0.004	53
Fetal rate (fawns per female)	1.45	0.07	<0.001	32
Fawn survival, 1-90 days	0.41	0.06	0.01	45
Fawn survival, 91-365 days	0.73	0.17	0.08	82
Adult survival, 1-365 days	0.90	0.005	<0.001	63

Table 3.3. Top-Ranked Vital Rates Models

Models within 2 AIC units of the top model are shown with parameter estimates and (standard errors), and difference in AICc score from top-ranked model. Models with uninformative predictive variables were eliminated from consideration, and are not shown.

Model Equation	β_1	β_2	β_3	$\Delta\ AICc$
Probability of pregnancy				
$P{\sim}\beta_1(Logged) + \beta_2\ (Winter_{(t-1)})$	2.49 (1.19)	-3.07 (1.55)	--	0
$P{\sim}\beta_1(Logged) + \beta_2\ (Winter_{(t-1)}) + \beta_3\ (Age)$	2.27 (1.22)	-2.99 (1.57)	1.24 (0.90)	0.12
Number of fetuses per female				
$F{\sim}\ 1$	--	--	--	0
$F \sim \beta_1(Age)$	0.20 (0.19)	--	--	1.24
$F \sim \beta_1(Mass)$	0.01 (0.02)	--	--	1.83
Fawn survival summer, 1-90 days				
$S(t)_S \sim \beta_1(Mass) + \beta_2(Sex)$	2.48 (0.97)	0.90 (0.56)	--	0
$S(t)_S \sim \beta_1(Mass)$	2.12 (0.92)	--	--	0.51
$S(t)_S \sim \beta_1(Mass) + \beta_2(Winter_{(t-1)})$	2.34 (0.95)	0.74 (0.62)	--	1.18
$S(t)_S \sim \beta_1(Mass) + \beta_2(B.date)$	2.08 (0.92)	0.03 (0.03)		1.65
$S(t)_S \sim \beta_1(Mass) + \beta_2(Sync)$	2.12 (0.91)	0.33 (0.40)	--	1.91
Fawn survival winter, 91-365 days				
$S(t)_w \sim \beta_1(Winter_t) + \beta_2(B.date)$	-3.27 (0.69)	-0.06 (0.02)	--	0
$S(t)_w \sim \beta_1(Winter_t) + \beta_2(B.date) + \beta_3(B.date * Winter_t)$	-1.60 (1.34)	0.02 (0.06)	-0.08 (0.06)	0.14
Adult survival 1-365 days				
$S(t) \sim \beta_1(Mass)$	-0.19 (0.07)	--	--	0
$S(t) \sim \beta_1(Age)$	-1.67 (0.74)	--	--	1.77

Table 3.4. Effects of Predictive Variables and Vital Rates on Population Dynamics

Vital rates are pregnancy, fetal rate, and survival for yearlings (*Py, Fy,* and *Sy*) and adults (*Pa, Fa,* and *Sa*), along with fawn survival in summer (Sf_S) and winter (Sf_W). Elasticities of vital rates, contributions of vital rates to variation in growth rate given a decrease of 2 times the process SD in vital rates (Cont.), and covariate elasticities given an increase $\boldsymbol{Ec_p}$ or decrease $\boldsymbol{Ec_n}$ of 2 times the process SD in predictive variables are shown.

Vital Rate	**Covariate**	**Cov. Mean (Process σ^2)**	**Vital Elasticity**	**Vital Cont.**	$\boldsymbol{Ec_p}$	$\boldsymbol{Ec_n}$
Pa	Logged	0.60 (0.00)	0.121	0.016	0	0
Pa	Winter(*t*-1)	0. 71 (0.42)	0.121	0.016	0.007	– 0.110
Py	Winter(*t*-1)	0. 71 (0.42)	0.025	0.001	0.007	– 0.110
Fy	--	--	0.025	<0.001	--	--
Fa	--	--	0.121	<0.001	--	--
Sf_S	Gender (F)	0.44 (<0.001)	0.150	0.061	0	0
Sf_S	Mass	2.63 (0.01)	0.150	0.061	0.062	– 0.067
Sf_W	Winter	0. 71 (0.42)	0.150	0.093	0.029	– 0.190
Sf_W	Birthdate	17.60 (0.25)	0.150	0.093	0.002	– 0.002
Sy	--	--	0.121	<0.001	--	--
Sa	--	--	0.587	<0.001	--	--

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CHAPTER 4. FEAR, FORAGE, AND FAWNS: NUTRITION AND PREDATION RISK DRIVE BEHAVIOR FOR FEMALE DEER[3]

4.1. ABSTRACT

Reproduction is a critical life-history period during which nutritional demands and risk of predation for parents and offspring are high. For ungulates, nutritional demands peak during late gestation and early lactation, declining as offspring age or die. Concurrently, predation risk to adult females increases in late gestation, then declines following birth of offspring. Additionally, female ungulates face risk to offspring, which represent a significant reproductive investment. In response, resource selection by adult female ungulates should vary through time within reproductive periods. Here, I test multiple hypotheses regarding female selection within the summer home range during three reproductive phases, 1) gestation, 2) lactation, and 3) recovery (after all offspring have died). Using mixed-effects logistic regression, I included interactive effects of time with bear risk, wolf risk, and forage in models for each reproductive phase. At the population level, adult females did not trade-off selection of forage with avoidance of risk, and predation risk and forage were negatively correlated among home ranges, indicating variation in home-range quality. Females increasingly avoided bear risk, relaxed avoidance of wolf risk, and increased selection for forage as parturition neared. After parturition, deer continued to avoid bear risk, increasingly avoided wolf risk, and increasingly selected for forage through time. If fawns died, females relaxed avoidance of bears, increased avoidance of wolves, and intensified selection for forage. Among individuals, females with more forage availability relaxed selection towards forage, whereas females with more predation risk intensified avoidance of predation risk. However, quality of home range did not predict spring body condition, which was instead correlated with selection of forage. A likely explanation is that deer density increases with habitat quality, leading to more generalized selection by deer in better home ranges, but that some deer make better choices than others regardless of home-range quality (i.e., individual heterogeneity).

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[3] Gilbert SL, Hundertmark KH, Person DK, Lindberg MS, Boyce MS (In Review) Fear, forage, and fawns: nutrition and predation risk drive behavior for female deer. Ecology.

4.2. INTRODUCTION

Behavior of animals can be strongly influenced by both fear and hunger as animals seek to optimize fitness (Creel & Christianson 2008; Ben-David et al. 2004). Animals can neither completely avoid predation risk nor use only the best-quality food, both because they lack perfect information about the landscape, and because forage and predation risk can be positively correlated due to predators seeking out prey species (Fortin et al. 2005, Hebblewhite & Merrill 2009). Instead, animals often must trade off predation risk and access to nutrition (Zera & Harshman 2001). Such trade offs are intensified during key life history phases such as reproduction, when predation risks, nutritional demands, and potential fitness rewards are high (Harshman & Zera 2007; Hebblewhite & Merrill 2009). In addition, current access to nutrition and exposure to predation risk can affect fitness in the future, through reduced likelihood of survival and future reproduction. As a result, trade-offs between parental predation risk, offspring predation risk, and access to nutrition vary by life-history strategy.

Trade-offs between current and future reproduction are most pronounced in long-lived, iteroparous species, where there are multiple future opportunities to breed and survival rates of reproductive adults are high (Gaillard & Yoccoz 2003). Current reproductive success depends on parental nutrition during gestation and provisioning of offspring (i.e., lactation) to ensure offspring are large, vigorous, and therefore likely to survive and avoid predators of offspring (Candolin 1998; Parker et al. 2009). However, future reproductive success depends on parental ability to replenish body reserves to levels that ensure survival and successful breeding at the next opportunity, and thus requires extra nutrition, as well as avoidance of predators of adults (Parker et al. 2009; Candolin 1998).

For most animals, predation risk and nutritional demands vary between and within reproductive phases. Nutritional demands increase through gestation or nest brooding (Tollefson et al. 2010; Oftedal 1985), peak during late gestation/brooding or while offspring are young and require parental provisioning (Oftedal 1985; Robbins & Robbins 1979), and diminish as offspring age. (Sadleir 1980). Likewise, females may become less able to elude predators or become more conspicuous during late gestation/brooding or offspring provisioning periods (Veasey et al. 2001), and offspring are often most vulnerable to predation just after birth (Carl &

Robbins 1988; Kaplan et al. 2008; Flint et al. 1995). Thus, trade-offs between predation risk and nutrition are likely to be time-dependent within each reproductive phase, as risks and demands fluctuate.

Predation risk and nutrition also vary spatially and temporally, independent of animals' life history phase (Creel & Christianson 2008; Godvik et al. 2009). Seasonal phenology of plants, competitors, alternative prey, and predators, along with habitat and topography, interact to create a fluctuating landscape of food and fear (Frair et al. 2005; Ben-David et al. 2004; Pierce et al. 2004). Reproductive animals must navigate this complex landscape, while responding to changing reproductive demands and risks. As a result, selection patterns of animals during reproduction should change through time within each reproductive phase, reflecting shifting trade-offs between current and future reproduction.

Adult female ungulates provide an excellent system for inquiry into time-dependent trade-offs during reproduction. Ungulates are long-lived, and females of most species raise and provision offspring without assistance from males. In addition, there is strong evidence for spatial trade-offs between risk and access to plant forage for numerous ungulate species, including during reproduction (Duquette et al. 2014; Hebblewhite & Merrill 2009; Long et al. 2009; Panzacchi et al. 2010). However, to my knowledge no studies have examined time dependence of spatial selection patterns within reproductive phase.

Here I focus on Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in Southeast Alaska, where adult female deer face predation by both wolves (*Canis lupus*) and black bears (*Ursus americanus*), whereas fawns face predation primarily by black bears. Wolves are relatively rare and highly cursorial, whereas black bears are more common and are mostly ambush predators. Prey animals can be more sensitive to predation risk from ambush rather than cursorial predators (Preisser et al. 2007; Schmitz 2008); Nevertheless, the abundance (Alaska Department of Fish and Game 2011) and omnivorous diet of bears likely make them difficult to avoid, particularly before the arrival of salmon in late summer (Campbell et al. 2012). In this complex system, pregnant females must balance risk to themselves with access to forage, whereas females with fawns must incorporate risk to self, risk to offspring, and access to nutrition into selection decisions. In contrast, if females lose offspring to predation, they face only risk to self and the need to recover nutritional condition to ensure future survival and

reproduction. These nutritional demands and predation risks change dynamically through each reproductive phase, and consequently, patterns of selection should vary across time.

Female deer are long-lived and typically reproduce annually. As a result, they should prioritize their own survival and nutritional condition over that of their offspring. Risk of wolf and bear predation is minimal for adult females during summer (Gilbert et al. 2014), although this could be in part a product of female trade-offs rather than of intrinsically low risk. In contrast, offspring predation risk is high at birth and sharply declines with age (Gilbert et al. 2014). As a result, a short period of bear avoidance while offspring are young coupled with peak energetic demands may temporarily compromise female foraging, but be worthwhile in terms of fitness due to the short duration of the effort and increase in fawn survival probability. Correspondingly, I hypothesize that pregnant deer should select for areas with abundant forage, should increasingly select for forage as parturition approaches and nutritional demands increase dramatically, and should reduce overlap with bears as parturition nears. Following parturition, I predict that deer with fawns prioritize survival and provisioning of fawns, selecting areas with minimal bear risk and abundant forage, and showing higher tolerance of wolf risk while fawns are young. As fawns age and risk of bear predation sharply declines (Gilbert et al. 2014), females should relax negative selection towards bear risk, instead selecting for higher forage values. If deer lose all offspring, they should first select strongly for high forage values in order to recover body reserves lost during pregnancy and lactation, but slowly relax this selection, potentially selecting against wolf risk more strongly instead as wolf packs become increasingly mobile during late summer (Person 2001).

In addition to these population-level hypotheses (Figure 4.1), I also predict that individual deer should exhibit a functional response to predation risk and forage availability. As the availability of a habitat and landscape attribute changes, animals may shift selection, resulting in a functional response (Knopff et al. 2014; Moreau et al. 2012; Godvik et al. 2009). For deer facing a trade-off between risks of predation and access to forage, once predation risk is sufficiently low or forage availability sufficiently high across the landscape, deer may focus on the competing component of the trade-off instead. Specifically, I predict that deer with low levels of predation risk available to them will reduce their avoidance of predation risk. Conversely, deer with high levels of forage availability should reduce their positive selection for forage because

nutritional demands can be satisfied in many locations. Finally, I predict that deer with better body condition should select less strongly for forage, allowing for increased avoidance of predators.

4.3. MATERIALS AND METHODS

4.3.1. Study Area

This study was carried out on the central portion of Prince of Wales Island, the largest island in the Alexander Archipelago of Southeast Alaska (Figure 4.2). The ecosystem is a coastal temperate rainforest, receiving >300 cm of precipitation a year (Gilbert et al. 2014).

4.3.2. Animal Capture and Handling

I captured adult female deer during spring (April- mid May) of 2010-2012. All captures were carried out in accordance with University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC #136040-14) regulations. Deer were captured on foot with the assistance of radio-telemetered darts (Pneu-Dart Inc., Williamsburg, PA), and fitted with GPS collars that recorded location every two hours for one year. In addition, body condition and pregnancy were assessed using a portable ultrasound machine (Sonosite Titan, Sonosite, Bothell, WA), and pregnant females were fitted with vaginal implant transmitters (VITs; Advanced Telemetry Systems, Isanti, MN). Signals from VITs within pregnant females were monitored 1-2 times per day to detect parturition, allowing for capture of neonatal fawns at birth sites. Subsequently, adult females were monitored 2-3 times per week for the remainder of the summer to detect mortality events. Across the three years of the study, I confirmed the birth of 45 fawns from GPS-collared females. Neonatal deer were fitted with break-away VHF or GPS collars, and gently restrained with eyes covered to reduce alarm during capture and subsequent handling. Handling time was <10 minutes per fawn, during which I measured mass and body morphology. Following capture, fawns were monitored 1-2 times per day for the remainder of the summer to detect mortality.

4.3.3. Spatial Predictive Variables: Forage Availability

I considered several measures of forage availability within landscapes that might influence patterns of selection by deer, including total forage biomass, forb biomass, digestible dry matter, and digestible protein. Type and quality of forage varied considerably between vegetation classes (Alaback 1982; Alaback & Saunders 2013) and several region-wide studies have focused on quantifying these differences, including abundance of species in each class (Hanley & Rogers 1989; Hanley et al. 2013). In addition, detailed studies of deer foraging ecology have resulted in a good understanding of seasonal energy balances and feeding preferences by species (Parker et al. 1993; Parker et al. 1996; Parker et al. 1999). Building on these studies, I generated spatially-explicit maps of forage abundance and quality across the landscape, using a GIS layer provided by the U.S. Forest Service and based on publically available US Forest Service "cover type" (i.e., vegetation class) and "size density" (i.e., timber volume) GIS layers (University of Alaska 2014). All measures of forage availability were based on databases from the Forage Resource Evaluation System for Habitat (FRESH) developed by the U.S. Forest Service (Hanley & Rogers 1989) and available online (Hanley et al. 2014). FRESH integrates available forage nutrition and deer physiological demands to produce derived measures of carrying capacity (i.e., "deer days"; Hanley & Rogers 1989), whereas I chose to simply use the original measures of available forage nutrition as predictive variables of deer selection. Measures of forage availability considered in competing models of deer selection included total biomass of all forage types, biomass of shrubs, biomass of forbs, total digestible dry matter, and total digestible protein. In addition, I standardized all forage availability rasters so that values ranged between 0 and 1, allowing comparison of coefficients with those of predation risk (relative probability of selection by predators), which also varied between 0 and 1. All spatial analysis was conducted in program R (R Core Development Team 2014). R packages used for spatial processing and analysis included rgdal (Keitt et al. 2010), sp (Pebesma & Bivand 2005; Bivand & Pebesma 2013), and raster (Hijmans et al. 2014).

4.3.4. Spatial Predictive Variables: Bear Predation Risk

Population-scale bear resource selection functions (RSF) were derived using generalized linear mixed models (GLMMs). They were based on GPS telemetry relocations of bears

monitored within the study area (Appendix). As with deer, bear resource selection was estimated during three seasons, based on phenology of food items thought to be important to bears (Appendix, Figures 4.8 and 4.9). Seasons for spatial analyses of bears were: 1) April 15 to the first recorded birthdate for sampled deer (i.e., 24 May), 2) after the first recorded birthdate but before salmon arrival in streams (i.e., 24 May – 31 July); and 3) after salmon arrival until end of summer (i.e., 1 August- 1 October). Spatial predictive variables included landscape, topographic, and vegetation classes (Appendix, Table 4.4). Resource selection functions that fit the location data best (Appendix, Table 4.5) were used to produce relative probability maps of seasonal resource selection by bears within the study area (Appendix, Figure 4.10).

4.3.5. Spatial Predictive Variables: Wolf Predation Risk

Habitat selection by wolves was characterized during a previous telemetry study of the wolf population on Prince of Wales Island from 1990-2004, in which 55 wolves were fitted with VHF collars to collect location data (Alaska Department of Fish & Game, unpublished data; Person & Russell 2008). The RSF that fit the location data best, based on AIC criteria, was applied to current GIS data layers to generate a map showing the relative probabilities of use by wolves. The best model for wolf habitat use in summer integrated vegetation class and landscape predictive variables at the scale of 1,000-m buffers around radio relocations (ADFG unpublished data). Predictive variables included diversity of vegetation classes (i.e., Shannon diversity index, Turner 1989), elevation, percentage of alpine vegetation type, percentage road, percentage stem exclusion clearcut (i.e., > 30 years in age), and an interaction between diversity and percent stem exclusion (Table 4.1). To create a GIS surface showing relative probability of selection for wolves, I updated the GIS layers used in the original wolf study so that habitat and landscape variables were the same.

4.3.6. Deer Resource Selection

I considered resource selection by deer relative to forage availability and risk of predation from bears and wolves within deer summer home ranges (i.e., 3rd order selection; Johnson 1980). I did not examine deer selection at the patch level (i.e., 4th order selection), typically implemented using step-selection functions and a 2-step modeling approach (Thurfjell et al.

2014), because sample sizes were quite uneven between individuals within seasons (e.g., some females lost fawns within a day of birth, whereas some retained fawns throughout the summer). I examined deer resource selection within three reproductive periods, defined by the reproductive history of each deer as 1) capture to parturition, 2) parturition to death of all fawns, and 3) death of all fawns until end of summer (1 October; Figure 4.1), and hereafter referred to as gestation, lactation, and recovery. If all fawns died at the birth site, the lactation period was absent for those females, which instead immediately transitioned to the recovery period. If a female retained live fawns until the end of summer, she did not transition to recovery.

4.3.7. Time Dependency of Selection

Within each reproductive period for each deer, I included time as a continuous covariate in models. Time was defined based on two key life history events, parturition and death of offspring (Figure 4.1). During gestation, time was defined as negative weeks until parturition (i.e., counting up to zero), whereas during lactation, time was defined as weeks since parturition (i.e., counting up from zero). If all fawns died, time was defined during the recovery phase as weeks since death of offspring. Time variables, representing time to or from a life-history event, were then included in selection functions as interactive terms with forage availability and predation risk, effectively allowing the strength and direction of selection to vary with time.

4.3.8. Selection Within Home Ranges

For analysis of selection at the home-range scale, habitat availability was defined for each deer individually, and was generated from the 98% MCP home range for each deer during the entire study period (Johnson 1980). For each used point, 5 available points were generated from within each deer's home range. I checked for collinearity between fixed effects in the model, and did not include terms that were highly correlated ($|r| > 0.6$). I fit GLMMs for each season, and considered random effects of individuals with structures that included an intercept term only, as well as random intercepts for bear and wolf predation risk and forage availability (Godvik et al. 2009; Moreau et al. 2012). In general, model structure took the following form:

$$w_{jt}(x_{ijt}) = \exp(\beta_0 + \gamma_{0j} + t * \beta_1 + (\beta_1 + \gamma_{1j})x_1 + \cdots + t * \beta_n + (\beta_n + \gamma_{nj})x_n \qquad \text{(eq.1)}$$

Where $w_j(x)$ is the relative probability of selection as a function of the predictive variables x_n and β_n are the coefficients associated with x_n, $t^*\beta_n$ is the interactive effect of time on β_n , and γ_{nj}, is the random coefficient for individual j that adjusts β_n. I first chose a structure for random effects based on information theoretic criteria (i.e., AIC score; Burnham & Anderson 2002), then determined which fixed effect terms for forage should be included (Bolker et al. 2008). I chose a random effect structure for the model by comparing models with the same fixed effects, in this case the full set of wolf risk, bear risk, and forage availability variables, while varying the random effects structure (i.e., a random intercept, plus all combinations of random coefficients for predictive variables). Once a best-fit random effect structure was selected, I included a suitable measure of forage availability from among the five measures considered based on AIC criteria among competing models that differed only by the forage variable chosen.

4.3.9. Analysis of Individual Variation in Selection

To determine if deer exhibited a functional response to either forage availability or predation risk, I tested for correlations between random coefficients of selection for each individual during gestation, lactation, and recovery against the averaged quantity of forage and predation risk across available points for each animal (Moreau et al. 2012). The random coefficient for each animal represents the difference between selection for that animal and the mean (fixed effect) coefficient for that covariate, so individual-level random coefficients can be used to examine the functional response of individuals (Moreau et al. 2012).

In addition, to explore if body condition affected strength of trade-offs between selection for forage and predation risk, I also tested for correlations between ingesta-free body fat (Cook et al. 2010) of adult female deer measured at capture and individual-level random coefficients of selection. In addition, I explored potential trade-offs between selection relative to forage and predation risk by correlating random coefficients of selection for bear and wolf risk with those for forage. Finally, I examined variation in home-range quality among individuals by correlating average quantity of forage against average quantity of bear and wolf predation risks for the available points of each individual. To see if overall quality of home ranges varied among individuals, and if strength of predator avoidance or forage selection increased with decreasing

home range quality (i.e., compensation in selection), I also developed metrics of home range quality and summed selection. I calculated home range quality as the averaged availability of forage across the home range, minus the summed average predation risk of bears and wolves across the home range. I calculated summed strength of selection for forage and against predation risk as the sum of the selection coefficient for forage and the absolute value of the sum of selection against predation, producing a metric for total strength of selection for forage and against predation. I tested for correlations using Kendall's tau, as availability within home ranges as well as individual coefficients of selection were often not normally distributed and sample sizes (i.e., numbers of individuals) were low. The low sample sizes raise the possibility of a type II error, in which real relationships are not identified. As a result, I report p values for all tests, but consider only correlations with $p < 0.05$ as demonstrating an association.

4.4. RESULTS

4.4.1. Deer Resource Selection Within the Home Range

For adult female deer in this study, GPS relocations were recorded once every 2 hours, resulting in an average of 372 relocations per deer during the gestation period (SD = 242), 685 relocations per deer during the lactation period (SD = 581), and 1,244 relocations per deer during the recovery period (SD = 110).

At the population level, deer during gestation selected locations with high forage availability, and did not respond consistently to wolf and bear predation risk, as indicated by large standard errors (Table 4.2). However, as time of parturition approached, deer selected more strongly for forage, avoided wolf risk less strongly, and avoided bear risk more strongly, as indicated by interaction terms with time (Figure 4.3). The best-supported measure of forage during gestation was total forage biomass (Table 4.3).

Following parturition, lactating deer changed patterns of selection relative to predation risk and forage availability. The best-supported measure of forage was forb biomass rather than total forage biomass (Table 4.3). Deer selected more strongly for forage than during gestation, with a small decrease in selection for forage through time. Deer selection toward habitats occupied by wolves remained variable, although deer slightly increased avoidance of wolf risk as

time progressed. In contrast, deer strongly avoided habitats selected by bears during lactation, but relaxed avoidance slightly as time progressed (Table 4.2; Figure 4.3).

If all fawns died, female selection patterns shifted yet again. During recovery, female deer increased selection for resource units high in forage compared with selection during gestation and lactation, and continued a general avoidance of wolves and bears. However, there was considerable variation among individual deer in selecting locations that avoided wolf activity. Through time following loss of fawns, deer selected less strongly for forage, and relaxed avoidance of predators, increasingly overlapping with bears and wolf RSFs. (Table 4.2; Figure 4.3).

4.4.2. Variation in Selection Among Individuals

There was substantial variation in selection patterns among individuals, as indicated by AIC-based support of random coefficients by individual for forage, relative risk of encountering bears, and risk of encountering wolves in addition to large standard errors for the fixed effects for these terms, and for a random intercept term. There was evidence of functional responses to availability of forage and predation risk, although effect direction and strength varied by reproductive stage (Figure 4.4). Furthermore, females with better body condition did not have higher levels of forage available to them within their home ranges (r = -0.16, p = 0.22 during gestation, r = -0.18, p = 0.20 during lactation, and r = -0.23, p = 0.24 during recovery). Rather, during lactation, females in better body condition selected more strongly for forage (r = 0.29, p = 0.04; Figure 4.5), indicating that components of fitness may be correlated for deer as in many other species (Blums et al. 2005; McLoughlin et al. 2006).

During gestation, deer appeared to select less strongly for forage when widely available within home ranges, as well as avoid predation risk more strongly (r = -0.31, p = 0.03 for bear risk; r = -0.34, p = 0.01 for wolf risk) when risk was high within home ranges (Figure 4.4, Figure 4.6a). Correspondingly, there was variation in home range quality, as within home ranges, average availability of forage was negatively correlated (r = -0.32, p =0.01) with average bear risk, although uncorrelated with wolf risk (r = -0.15, p = 0.27; Figure 4.7). Body condition was correlated with selection of forage (r = 0.24, p = 0.07) and wolf risk (r = -0.24, p = 0.06) but not bear risk (r = 0.13, p = 0.32; Figure 4.5). Evidence for trade-offs between forage and risk was

lacking (Figure 4.6a), as there were not positive correlations between selection for forage and bear risk (r = - 0.08, p = 0.55) or wolf risk (r = -0.30, p = 0.02).

As deer transitioned to lactation following the birth of fawns, there continued to be a functional response to forage availability (r = -0.26, p = 0.06), as well as to bear and wolf risk (r = -0.31, p = 0.03 for bear risk; r = -0.34, p = 0.01 for wolf risk; Figure 4.4). There continued to be no selection trade-offs evident, with selection for forage and predation risk not positively correlated (r = 0.16, p = 0.26 for bear risk, and r = -0.16, p = 0.26 for wolf risk; Figure 4.6). Deer in better body condition selected more strongly for forage (r = 0.29 , p = 0.04). Functional responses became more pronounced during recovery, with deer selecting more strongly for forage (r = -0.54, p < 0.01), and against bear risk (r = -0.77, p < 0.01) and wolf risk (r = -0.67, p < 0.01) when average availability was high within home ranges. However, no trade-offs were evident based on a lack of positive correlation between individual selection for forage and predation risk (r = -0.12, p = 0.56 for bear risk, and r = -0.22, p = 0.28 for wolf risk). Females in better body condition selected more strongly against wolf risk (r = -0.37, p = 0.06).

4.5. DISCUSSION

I found evidence that deer optimize selection within home ranges to minimize risk to themselves and to offspring, and maximize access to forage. However, because wolf and bear probability of use was not strongly linked to forage measures, deer did not face stark trade-offs (Figure 4.6; rather, deer shifted selection priorities through reproductive phases in order to maximize current fitness (i.e., fawn survival) when fawns were alive, then switched to maximizing future fitness (i.e., adult survival and recovery of body condition) once fawns were dead. Moreover, deer modified the strength of selection for forage and against predation risk based on the composition of the home range, partitioning from predation risk more strongly when predation risk was high within the home range, and relaxing selection for forage when forage was abundant across the home range (Figure 4.7). In landscapes with widely distributed and highly abundant forage such as the study area, large trade-offs between risk and forage may be minimal for reproductive animals, instead leading to plastic behavioral solutions, in which animals vary strength of selection and avoidance through time and based on the composition of the local landscape.

Deer adjusted selection relative to forage and predation risk differently during each reproductive phase, and varied selection patterns across time within each phase. As I had hypothesized (Figure 4.1, Figure 4.3), deer selected strongly for forage, particularly during times of increased nutritional demand during late gestation and early lactation (Barboza et al. 2009; Parker et al. 2009; Oftedal 1985). Deer decreased selection for forage while increasing avoidance of predators when nutritional demands eased during late lactation and late recovery. Avoidance of predation was most striking during early lactation, when deer strongly avoided areas preferred by black bears, likely to reduce risk of predation on fawns. Overlap with bears was even lower during recovery; this was presumably due to the dramatic shift in bear distribution, because bears strongly selected streams where salmon spawned (Appendix, Figure 4.10), rather than active avoidance by deer. However, given the high predation rate of bears on fawns (Gilbert et al., in review), deer are clearly unable to fully partition themselves from bear risk, possibly due to active selection of deer habitat by bears either seeking fawns or specific plant forage species (Bastille-Rousseau et al. 2011). In addition, the wolf RSF, based on limited telemetry data, did not take into account shifts in wolf behavior from spring denning season through late summer, during which wolves would likely begin to track the distribution of deer as pups become increasingly independent.

Patterns of selection among individuals varied by availability of forage and risk, as well as by spring body condition. Deer selected less strongly for forage when forage availability was high, indicating that patterns of deer selection may vary across productivity gradients. Alternatively, this functional response could be an artifact of the models, in which selection for important rare commodities may be more easily detected and inflated compared to selection of readily available but still important commodities. Likewise, deer that occupied high-risk home ranges partitioned themselves from predation risk by selecting more strongly against predation risk. The exception to this pattern of anti-predator behavior was during lactation, when deer displayed a functional response to average level (i.e., availability) of wolf risk but not to bear risk within the home-range, with increased wolf risk in home-ranges resulting in greater aversion to habitat preferred by wolves. Although the population-level coefficient of selection for bear risk was highly negative during lactation, there was a high degree of variability among individual deer, potentially reflecting differences in level of maternal experience (i.e., individual

heterogeneity), in local bear density and therefore true risk, or in quality of home ranges and thus need for bear avoidance (Figure 4.7). Because I did not have spatially explicit measures of bear density, and only a small fraction of the bear population was radio-collared, I could not estimate true predation risk from bears. A comparison of sites where bears preyed on fawns with matching randomly located sites could prove illuminating in this regard.

Selection relative to wolf risk was highly variable (i.e., large standard errors of coefficients) throughout the seasons, and was slightly positive during gestation and lactation, and slightly negative during the recovery period. Although deer did not avoid wolves during gestation as I had hypothesized, the relative response of deer to wolf risk through time followed the trends I predicted, with deer reducing overlap with wolves as parturition neared and continued to reduce overlap as fawns aged. Failure of deer to avoid wolves during gestation and lactation could be because wolves are not as active across the landscape during this time period. Wolves constrict their movements during pup-rearing season; on Prince of Wales island, average size of pack home range declined from 259 km^2 in winter to 104 km^2 during pup-rearing (15 April-15 August; Person 2001), with the likely result that for many deer, probability of encountering a wolf during early summer may be low. In addition, behavioral responses of cervids to cursorial predators such as wolves appears to be prompted by current predator activity levels at a particular location, rather than habitat cues alone (Creel et al. 2005; Kuijper et al. 2014; Middleton et al. 2013; Chamaillé-Jammes et al. 2014). Wolf numbers in the study area have been reduced due to human harvest (Alaska Department of Fish and Game 2014), and annual predation rates of adult deer in the study area have declined from 7% of adult female deer during 2000-2004 (Person et al. 2009) to 0% during this study. As a result, deer may not respond as strongly to landscape cues associated with wolf risk unless accompanied by wolf activity (Chamaillé-Jammes et al. 2014), or may respond only if in good body condition or if exposed to high levels of wolf risk in the greater home range (i.e., functional responses, Figs. 4.4). I found some evidence for females in better body condition increasingly avoiding wolves (Figure 4.5), although this explanation is confounded with the alternative explanation that high-quality females occupy low-risk, high-forage home ranges, and thus have higher body condition (Figure 4.7).

Female preference for forb, shrub, or total biomass varied by reproductive phase, with selection best predicted by total biomass during gestation, and by forb biomass during lactation and recovery. Gestation spans the period of spring forage emergence, and deer use both winter forages (i.e., woody browse, evergreen forbs, and fern rhizomes; Parker et al. 1999) and emergent, preferred spring and summer forages (i.e., deciduous forbs; Parker et al. 1999). Total biomass combines both winter and summer forage classes, explaining the preference of deer during gestation. In contrast, nutritional demands peak during lactation, while adult deer are limited by foraging time and rumen turnover rate (Barboza & Bowyer 2000; Barboza & Bowyer 2001). As a result, high-quality, easily digested forages are selected, predominantly forbs (Parker et al. 1999; Parker et al. 1996; Parker et al. 2009), as confirmed by the results.

There are a number of fruitful lines of inquiry that could productively build on these results. An improved understanding of predator resource selection, which is also likely time-dependent, would improve future predator-prey modeling efforts, as would better metrics of predation risk that incorporate wolf pack home ranges, and bear and wolf densities. In addition, temporal partitioning within the dial cycle is possible, and is a clear avenue for future research. Moreover, female deer and fawns may use a range of scale-dependent anti-predator behaviors (Panzacchi et al. 2010; Van Moorter et al. 2009), while I consider selection only at the home-range scale. Finally, I found support for functional responses, but a framework for robust statistical analysis of derived estimates such as RSF coefficients is currently lacking; an improved spatial modeling framework that can explicitly include functional responses would greatly improve our understanding of the spatial components of evolutionary and ecological decision-making by animals.

Here, I demonstrate the dynamic, time-dependent, and availability-dependent ways in which deer chose habitats during a critical life-history period. Deer do not trade off predation risk against forage in this system, but rather prioritize selection in a time-dependent way through the reproductive cycle as nutritional needs peak and decline, and predation risk to self and offspring fluctuate. Beyond these population-level patterns, individual differences in behavior and home-range quality explain much of the variance in selection. Quality of female home ranges varied, with high average levels of available forage correlated with lower average levels of predation risk (Figure 4.7). In high quality home-ranges, females relaxed selection for forage

and avoidance of predation. Sitka black-tailed deer are highly philopatric, typically establishing relatively small, stable home ranges close to that of their mother (Colson et al. 2013). As a result, the quality of individual females is likely in part the result of both high-quality home ranges of individuals (McLoughlin et al. 2007) and high-quality grandmaternal home ranges (McLoughlin et al. 2008). However, quality of home range does not necessarily equate to quality of females. I found that higher spring body fat was linked to stronger selection for forage within the home range (Figure 4.5), but not to availability of forage within the home range. A likely explanation of the results is that there is a gradient of deer density, with lower density in low-quality habitat types. I were not able to measure deer density within female home ranges during this study, however decreased deer density in lower-quality habitats has been documented within the study area (Brinkman et al. 2011). High density leads to increased competition for resources, removing fitness benefits of selection for high-quality habitats (Mcloughlin et al. 2006; McLoughlin et al. 2007) and leading to selection for lower-quality habitats (Mcloughlin et al. 2006; van Beest et al. 2014). Hence, increased density in high-quality areas could explain the relaxed selection for forage and against predation observed in females occupying high-quality home ranges, as well as the lack of correlation between forage levels within the home range and female body condition. Across the gradient of habitat quality and presumably deer density, some deer appear to make better choices than others, resulting in differences in body condition and likely in fitness correlates.

4.6. ACKNOWLEDGEMENTS

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4.7. FIGURES

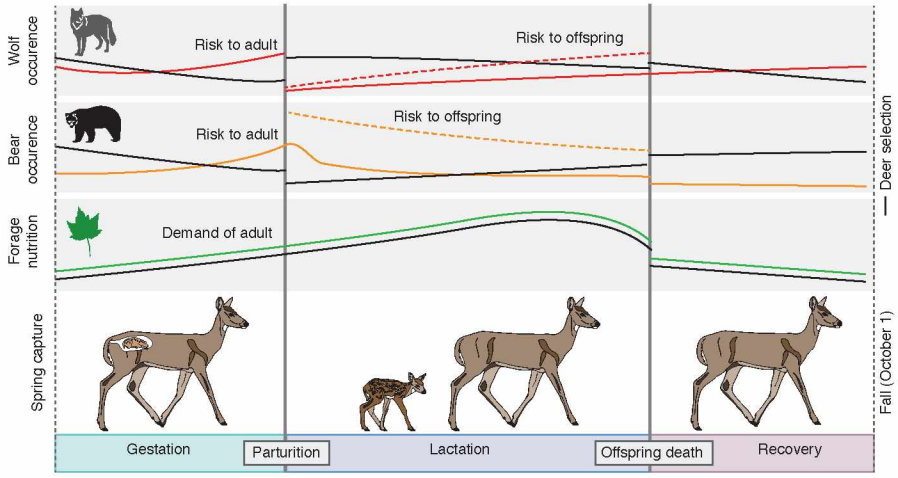

Figure 4.1. Deer reproductive seasons and selection hypotheses.

Deer reproductive seasons for this study, defined by parturition and offspring death and bracketed by spring capture and the onset of fall (October 1). Hypothesized patterns of adult female deer selection (solid black line) relative to forage availability (green line), predation risk from bears (orange lines) and wolves (red lines), are shown, with predation risk to adults and fawns shown as solid and dashed lines, respectively.

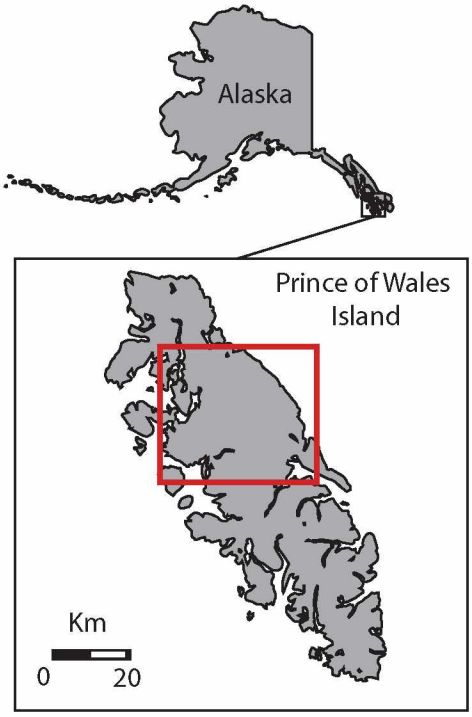

Figure 4.2. Study Area Map.

The study area (red box), located on the central portion of Prince of Wales Island in Southeast Alaska.

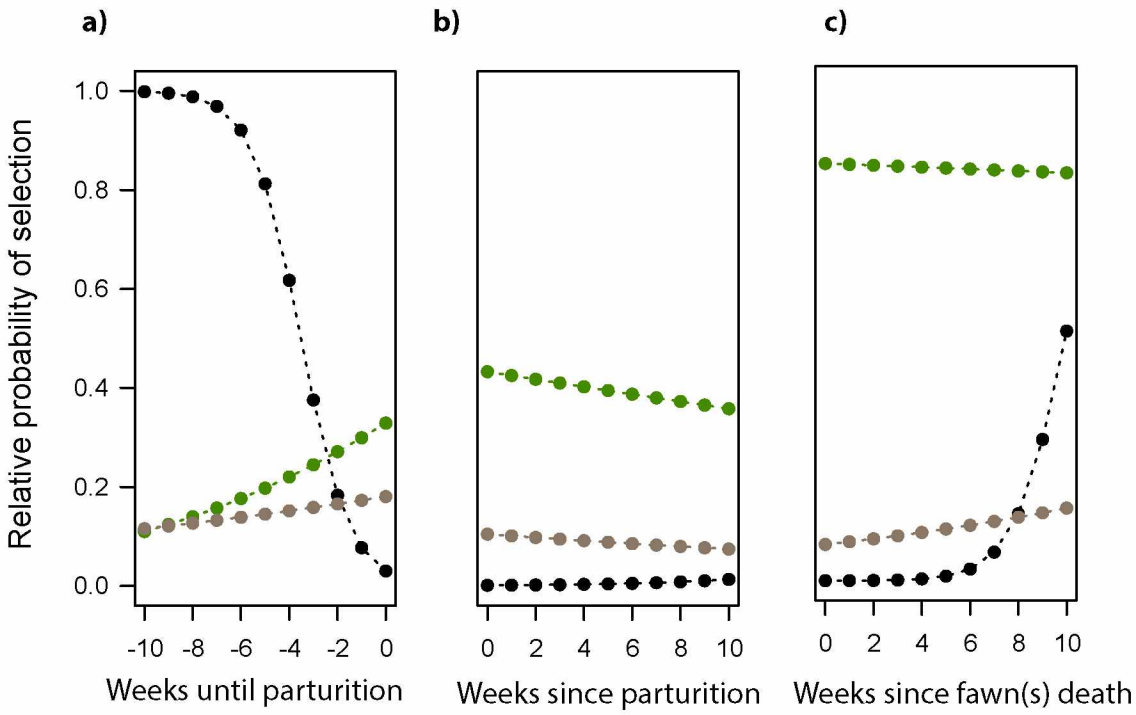

Figure 4.3. Population-Level Selection by Deer for Forage, Bear Predation Risk, and Wolf Predation Risk Through Time.

Effects of time are shown by reproductive seasons a) gestation, b) lactation, and c) recovery. To predict the effects of time, levels of the covariate were set at the seasonal maximum value, while other covariates were held at seasonal mean values and time was varied.

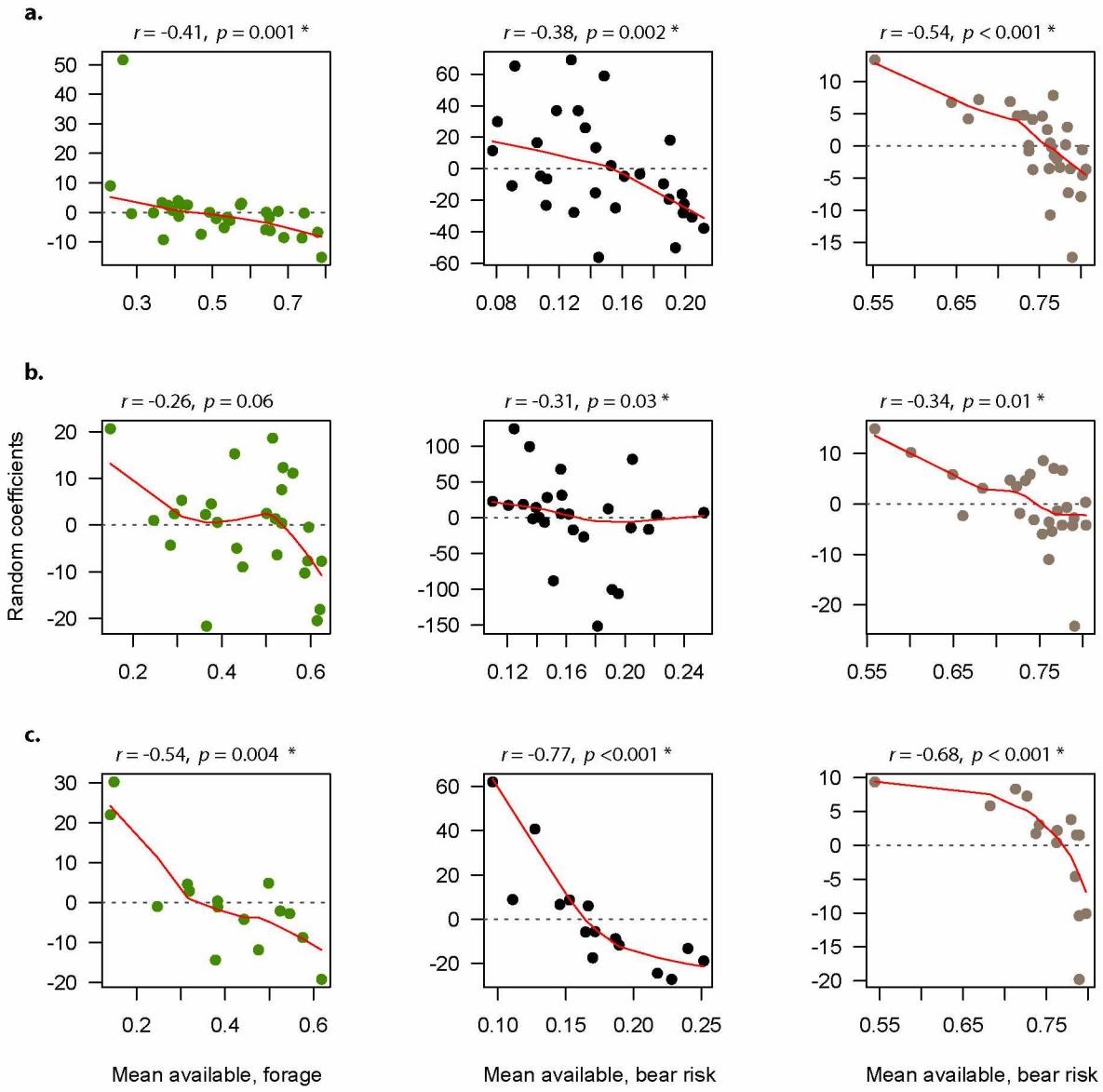

Figure 4.4. Functional Responses in Selection of Individual Deer.

Functional responses of adult female deer selection to availability of forage, bear predation risk, and wolf predation risk within individual home ranges, for the reproductive seasons **a)** gestation, **b)** lactation, and **c)** recovery. The functional response is illustrated by random coefficients for individuals, indicating the difference from fixed effect coefficients (i.e., population mean). Smoothed lines fit with Lowess models are shown in red. Kendall's rank tests for correlation *r*-scores and *p*-values are shown above, with * indicating $p < 0.05$.

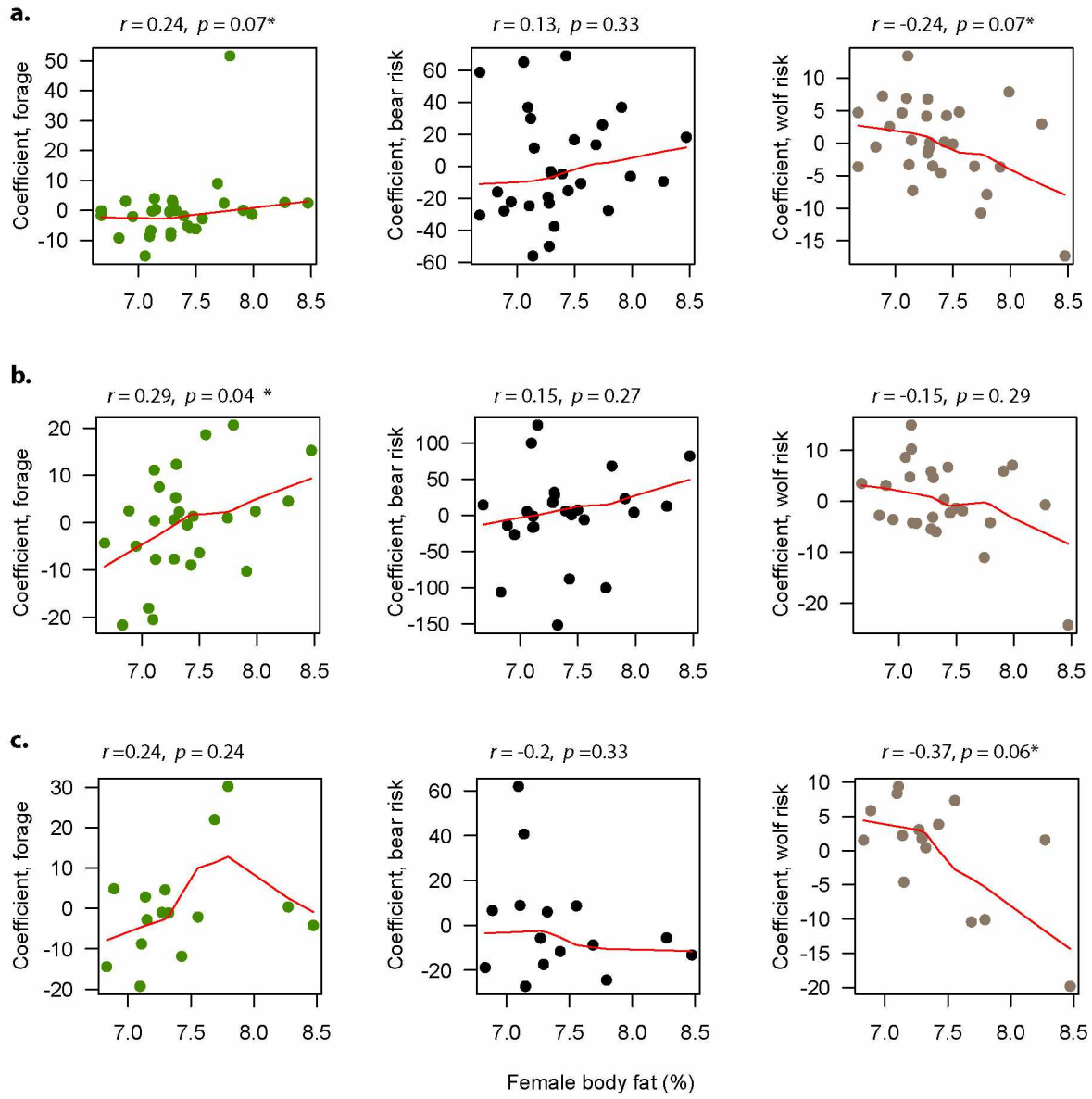

Figure 4.5. Effects of Body Condition on Individual Selection of Deer.

Effect of body condition (ingesta-free body fat %) of adult female deer in spring on subsequent selection for forage, bear predation risk, and wolf predation risk, for the reproductive seasons **a)** gestation, **b)** lactation, and **c)** recovery. Differences in selection are shown as random coefficients for individuals, indicating the difference from fixed effect coefficients (i.e., population mean). Smoothed lines fit with Lowess models are shown in red. Kendall's rank tests for correlation *r*-scores and *p*-values are shown above, with * indicating $p < 0.05$.

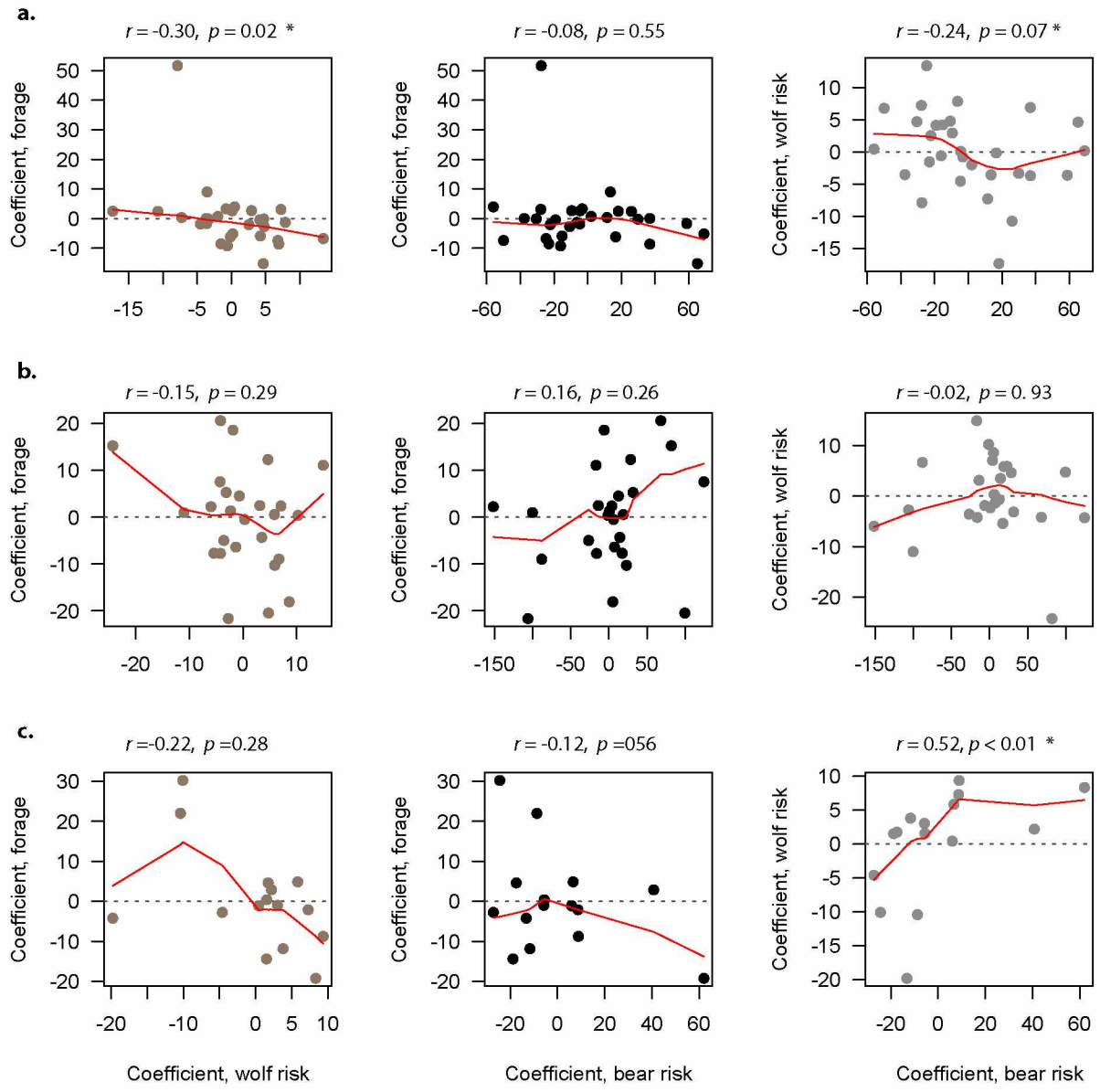

Figure 4.6. Potential Trade-Offs Between Forage and Predation Risk for Deer.

Potential trade-offs for adult female deer between forage, bear predation risk and wolf predation risk, illustrated by correlations between individual selection for forage and predation risk. Shown are individual differences in selection coefficients during a) gestation, b) lactation, and c) recovery. Smoothed lines fit with Lowess models are shown in red. Kendall's rank tests for correlation *r*-scores and *p*-values are shown above, with * indicating $p < 0.10$.

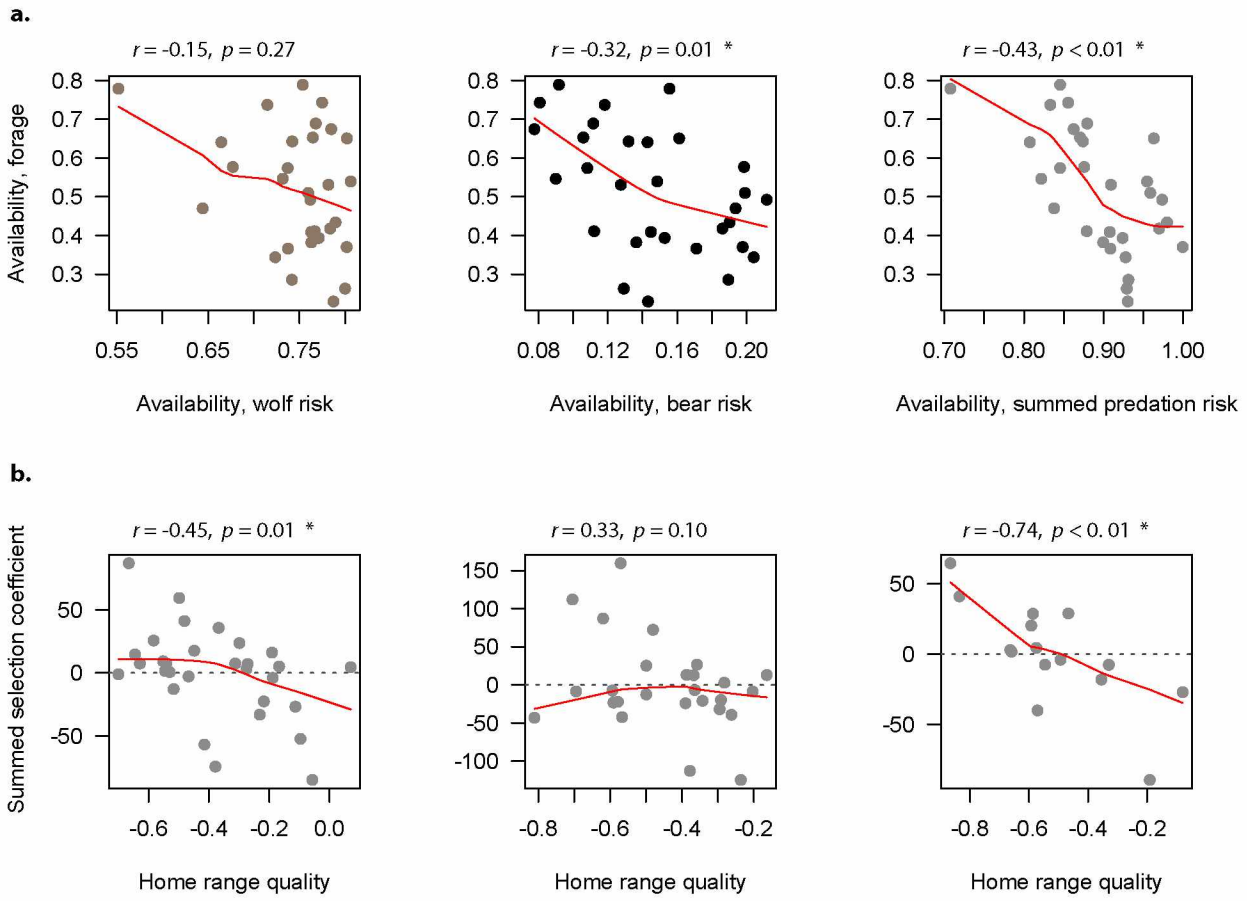

Figure 4.7. Differences in Home Range Quality for Deer and Effects on Selection. Differences in average forage and predation risk among deer home ranges, show for a) total forage biomass versus wolf risk, bear risk, and summed wolf and bear risk; and b) effect of home range quality (i.e., availability of forage + availability of bear risk + availability of wolf risk) on strength of deer avoidance of predators and selection of forage, as depicted by summed selection coefficients (i.e., |selection of predation risk | + selection of forage). Smoothed lines fit with Lowess models are shown in red. Kendall's rank tests for correlation *r*-scores and *p*-values are shown above, with * indicating $p < 0.10$.

4.8. TABLES

Table 4.1. Coefficients of Wolf Resource Selection

Coefficients for resource selection by wolves in summer at the 1000-m scale, with standard errors and p-values.

Variable	β Coefficient	*S.E.*	*p* value
Percent alpine	-0.111	0.061	0.072
Percent road	-0.180	0.032	0.001
Diversity	1.984	0.565	0.001
Elevation	-0.002	<0.001	0.001
Diversity x Percent Stem Exclusion	0.029	0.008	0.001

Table 4.2. Coefficients of Deer Resource Selection at the Population Level

Coefficients for forage, wolf risk, and bear risk are shown with standard errors in parentheses, and interactive effects with time are denoted as **time*. During gestation, time denotes negative weeks until parturition (counting upwards to zero), while during lactation and recovery, time denotes days since fawn birth or fawn death.

	Gestation	**Lactation**	**Recovery**
Model Terms	**β (SE)**	**β (SE)**	**β (SE)**
Forage	2.03 (1.79)	3.87 (1.55)	6.72 (2.17)
Forage*time	0.20 (0.02)	-0.08 (0.01)	-0.11 (0.01)
Wolf risk	0.87 (1.11)	0.64 (1.37)	-1.23 (1.44)
Wolf*time	0.40 (0.06)	-0.19 (0.02)	0.13 (0.02)
Bear risk	-3.20 (3.36)	-7.27 (2.11)	-12.01 (2.98)
Bear*time	-1.86 (0.09)	0.38 (0.04)	1.51 (0.05)
Time	0.19 (0.05)	0.12 (0.02)	-0.26 (0.02)

Table 4.3. Competing Resource Selection Models with Different Measures of Forage. Models are shown with AIC scores. Model structure was held constant, with random coefficients and fixed effects for bear predation risk, wolf predation risk, and forage availability, as well as fixed effects for time interactions for all 3 covariates.

Forage measure	**Gestation AIC**	**Lactation AIC**	**Recovery AIC**
Total forage biomass	40,428	72,777	62,599
Biomass of forbs	40,799	71,085	61,284
Biomass of shrubs	41,587	73,574	67,778
Digestible dry matter	40,761	73,080	62,999
Digestible protein	40,905	72,168	62,440

4.9. APPENDIX

Appendix. Methods and results from analysis of habitat selection of black bears, used to generate bear predation risk maps for deer selection models

Study Area

Similar to the study area for deer, the study area was located on the central portion of Prince of Wales Island, which is the largest island in the Alexander Archipelago of Southeast Alaska (Figure 4.2). However, the study area was somewhat larger than for deer, as black bears have larger home ranges than deer and were originally captured across a larger geographical area (Appendix, Figure 4.8).

Animal Capture and Handling

I captured 31 adult black bears during late spring and early summer (May-July) from 2009-2012, and re-captured 19 individuals in subsequent years in order to re-collar them, resulting in 53 bear-years of data. All bear captures were carried out by Alaska Department of Fish and Game personnel. Bears were captured in modified Aldrich foot snares in elevated bucket sets, or free-range darted with the assistance of trained hounds. While chemically immobilized, bears were fitted with GPS collars, a tooth was extracted for age determination, and morphological measurements and blood and hair samples were collected.

GPS Data

GPS relocations of black bears were recorded every 30 minutes, and bears with fewer than 2 weeks worth of relocations within a given season (Appendix, Figure 4.8) were excluded. This resulted in an average of 1380 relocations per bear during the pre-fawn period (SD = 386), 2104 relocations per bear during the pre-salmon period (SD = 642), and 2121 relocations per bear during the post-salmon period (SD = 481).

Landscape Covariates

Landscape, habitat, and forage variables used in spatial analyses (Appendix, Table 4.4) were derived from GIS layers provided by the U.S. Forest Service (e.g., "covertype" and "size

density" layers describing forest type and management,). Because these spatial variables occurred on different scales (e.g., binary habitat values versus measures of forage biomass per area), covariates of selection could not be directly compared as an indicator of relative strength of selection. To make variable coefficients comparable, I standardized raster layers so that values varied between zero and one. In addition, the USFS original layers were derived from aerial photographs, from which polygons and subsequently rasters were produced. Due to the inherent error associated with this classification process, I converted binary variables to average values within 100-m circular moving windows, resulting in smoothed rasters composed of percentage values that varied between 0 and 1. All spatial analysis was conducted in program R (R Core Development Team 2014). R packages used for spatial processing and analysis included rgdal (Keitt et al. 2010), sp (Pebesma & Bivand 2005; Bivand & Pebesma 2013), and raster (Greenberg et al. 2014).

Bear Resource Selection Model Development

I developed population-level models of bear resource selection using generalized linear mixed models (GLMMs), with individual bear as a random effect and a logistic link function (Gillies et al. 2006; Fieberg et al. 2010). Models were developed in the lme4 package for program R. I used a GLMM framework because sample sizes differed between bears within seasons, and because the intention was to generate a population-level equation in order to create a relative probability of selection per GIS layer for use as a covariate in deer selection models rather than to analyze variability of selection among bears.

Bear resource selection was analyzed in three periods (Appendix, Figure 4.9), although as bear capture dates were highly variable, period 1 was defined as beginning on 15 April of each year, a time definitively after bear emergence from winter dens (Alaska Department of Fish and Game, unpublished data). In addition, black bears on Prince of Wales Island use salmon extensively, so period 2 was defined relative to salmon arrival. Salmon runs on Prince of Wales Island are dominated by pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon, which arrive in freshwater streams beginning in early August, peaking in August and September (Campbell et al. 2012). Therefore, bear seasons for RSFs were: 1) from April 15 to the first recorded birthdate for sampled deer (i.e., 24 May), 2) after the first recorded birthdate but before

salmon arrival in streams (i.e., 24 May – 31 July); and 3) after salmon arrival until end of summer (1 August- 1 October). Available points used in bear seasonal RSFs were generated within a 98% minimum convex polygon (MCP) summer home range for each bear (Johnson 1980), as the intention was inference regarding seasonal relative probability of use by bears. For each used point, 5 available points were randomly generated from within the study area.

I selected landscape and habitat covariates based on published studies of bear habitat selection in similar ecosystems (Davis et al. 2006; Nielsen et al. 2004), as black bears are not well studied in Southeast Alaska. Habitat covariates considered for bears included the measures of forage availability discussed above, and landcover described by nine types, including young clearcuts (<30 years since cut), old clearcuts (>30 years), low-, medium-, and high-volume old-growth forest, alpine, open habitats (i.e., meadows, grassland estuaries, and muskeg heaths), and other non-forested landcover (i.e., remaining, low-abundance habitats; Appendix, Table 4.4). Landscape covariates considered road density, edge density, and density of streams and rivers with anadramous fish runs. Topographic variables considered were elevation and slope, as well as squared versions of these terms in order to evaluate potential selection for intermediate values via quadratic terms.

I evaluated models of bear resource selection in a hierarchical fashion. For each season, I first developed separate groups of models for topographical, landscape (at both the 100-m and 1000-m scales), and land cover variables that included all subsets of variables within each group, and selected top models from each group comprised of models within 2 AIC units of the top model within the group. I then developed a final model set comprised of all combinations of top models from each group.

Bear Resource Selection Results

Bear resource selection patterns differed between the pre-fawn, pre-salmon, and post-salmon summer seasons (Appendix, Table 4.5, Figure 4.10). During the pre-fawn season, bear selection was best explained by a global model, containing all landscape variables (i.e., road, edge, and stream density, with densities calculated at 1000-m scale), all topographic variables (i.e., elevation and slope), and a slightly reduced set of land cover (habitat) variables (Appendix, Table 4.5). Bears selected positively for road and edge density, slope, all ages of clearcut forest

including thinned stands, and low- and high-volume old-growth forest, with largest magnitude of coefficients for slope (β = 4.31, SE = 0.10), edge density (β = 2.86, SE = 0.10), and road density (β = 1.81, SE = 0.08). In contrast, bears selected against stream density, elevation, and alpine and open vegetated habitats, with largest magnitude of coefficients for alpine habitat (β = -2.56, SE = 0.26), and open vegetated habitat (β = -1.84, SE = 0.24).

Patterns of spatial selection shifted during the pre-salmon season (Appendix, Figure 4.8 b). The best-fit model was complex, lacking only low volume and thinned-cut forest habitats. As during the pre-fawn season, bears selected positively for densities of roads and edges, as well as for steeper slopes. In addition, bears positively selected for elevation and stream density. However, bears selected against all habitat types except for young-cut forest, which they positively selected for. The largest magnitude coefficients were for edge density (β = 1.60, SE = 0.05), road density (β = 1.13, SE = 0.04), and slope (β = 1.07, SE = 0.06), indicating landscape variables strongly influence bear selection.

In contrast to the pre-fawn and pre-salmon seasons, bear selection during the post-salmon season was largely driven by a single variable, stream density (β = 1.07, SE = 0.06; Appendix, Figure 4.8 c). In addition, bears selected steeper slopes, and open vegetated habitats. Bears avoided thinned-cut forest, alpine, and low- and medium-volume forest, and selected for lower elevations and lower road densities.

Figures, Appendix

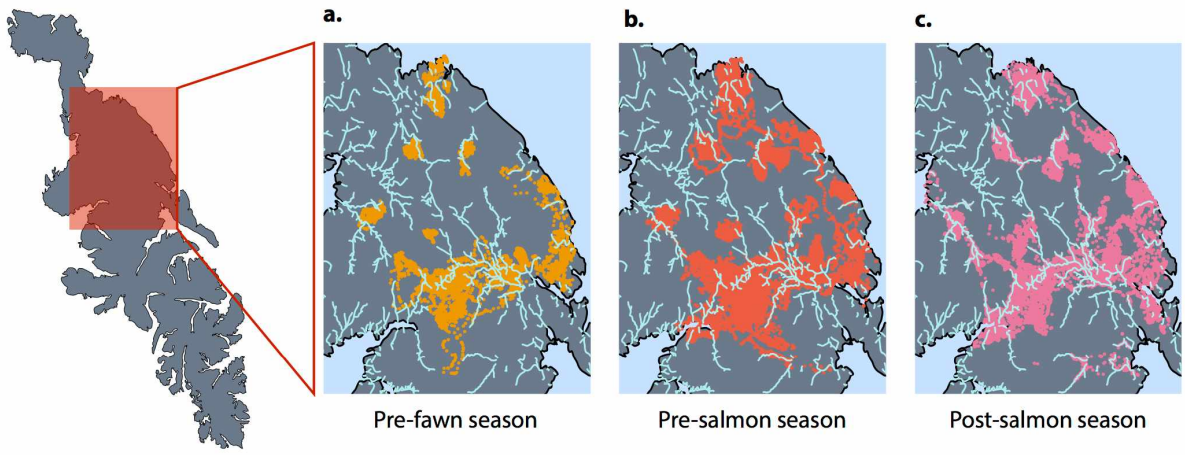

Figure 4.8. Bear Relocations on Central Prince of Wales Island by Season.

Relocations in the a) pre-fawn season (April 15- May24), b) pre-salmon season (May 25- July 31), and c) post-salmon season (August 1- October 1).

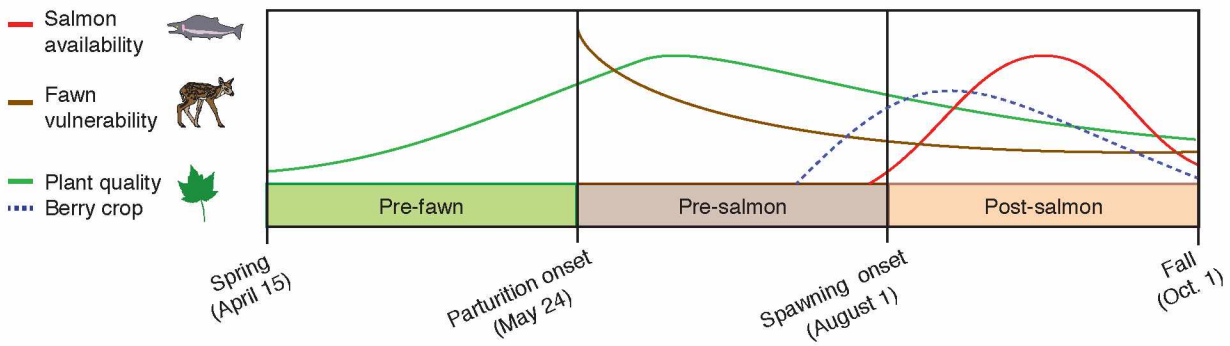

Figure 4.9. Schematic Diagram of Bear Resource Selection by Seasons.

Seasons for bear resource selection analysis, defined based on key forage items of plants, deer fawns, and salmon, divide bear analyses into three periods, I) pre-fawn season (April 15-May24), II) pre-salmon season (May 25- July 31), and III) post-salmon season (August 1-October 1).

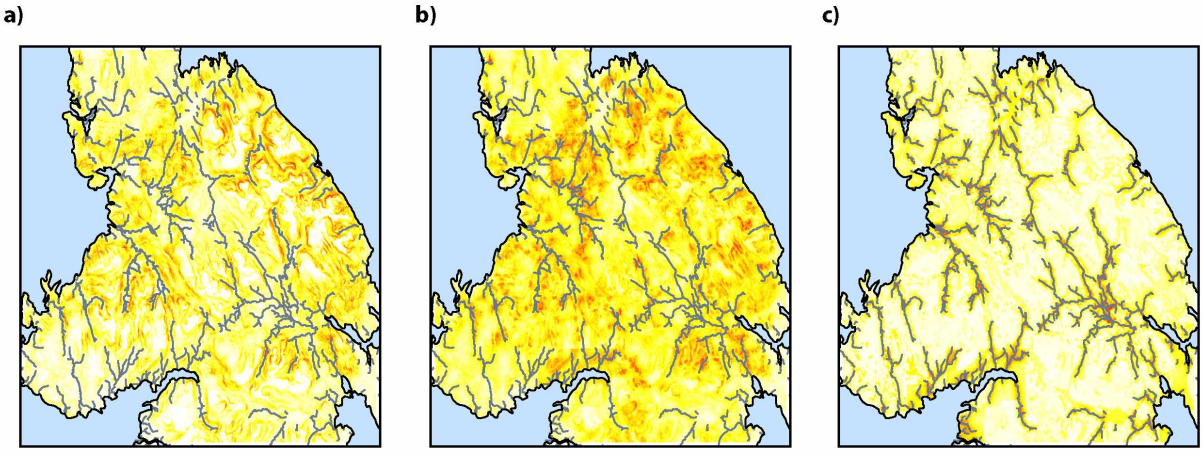

Figure 4.10. Maps of Bear Relative Probability of Selection.

Relative probability of selection translated to RSF surfaces, for bears in the study area during **a)** pre-fawn season, **b)** pre-salmon season, and **c)** post-salmon season. White to red color gradation indicates low (zero) to high (1) relative probabilities of selection.

Tables, Appendix

Table 4.4. Spatial Variables Used in Bear Resource Selection Models

Spatial variables, including topographic variables, landscape characteristics, and Land cover (habitat) types, included in bear resource selection analysis.

Variable	Description
Topography	
Elevation	Elevation above sea level, in meters
Slope	Slope, in degrees
Landscape	
Stream density	Steam reaches that contain spawning habitat for salmon
Road density	Density of all road types, computed using a kernel density estimate at 100-m at 1000-m scales
Edge density	Density of edges between habitat polygons, computed using a kernel density estimate at 100-m at 1000-m scales
Land cover	
Young cut forest	Young clearcut forest, 0-30 years after harvest
Old cut forest	Old clearcut forest, > 30 years after harvest
Thinned forest	Logged habitat stands that have undergone pre-commercial thinning, in which at least 50% of the stand area was thinned
Low volume forest	Forest classified as unproductive
Medium volume forest	Forest classified as size density class 4 or 5
High volume forest	Forest classified as size density class 6 or 7
Alpine	Alpine habitat, including high elevation sparse forest
Open vegetated	Open vegetated habitats comprised of muskeg heaths, and wetland, estuary, and beach grasslands
Other non-forest	Habitats including freshwater lakes, non-salmon stream reaches, alder brush, rock, ice, urban areas, and privately owned lands

Table 4.5. Coefficients of Top-Ranked Bear Selection Model for Each Season

Fixed effects of best-supported models of bear resource selection for each season, shown with β coefficients and standard errors.

	β (SE)		
Variable	**Season 1**	**Season 2**	**Season 3**
Intercept	-3.92 (0.08)	-2.78 (0.03)	-1.41 (0.06)
Slope	4.32 (0.09)	1.07 (0.06)	0.38 (0.07)
Elevation	-1.25 (0.16)	1.00 (0.08)	-1.57 (0.10)
Stream density (1000m)	-1.25 (0.09)	0.43 (0.04)	3.16 (0.05)
Road density (1000m)	1.81 (0.08)	1.13 (0.04)	-0.70 (0.05)
Edge density (1000m)	2.86 (0.10)	1.60 (0.05)	--
Young cut forest	0.35 (0.04)	0.34 (0.02)	--
Old cut forest	0.73 (0.06)	-0.15 (0.03)	--
Thinned forest	0.82 (0.05)	--	-0.31 (0.03)
Low volume forest	0.13 (0.05)	--	-1.22 (0.03)
Med. volume forest	--	-0.39 (0.02)	-1.02 (0.02)
High volume forest	0.42 (0.05)	-0.17 (0.02)	--
Alpine	-2.56 (0.27)	-0.55 (0.05)	-0.58 (0.07)
Open vegetated	-1.84 (0.24)	-0.11 (0.06)	0.80 (0.04)

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CHAPTER 5. SEASON OF SCARCITY: DYNAMIC EFFECTS OF SNOW DEPTH ON WINTER HABITAT SELECTION OF DEER IN A TIMBER-HARVESTED LANDSCAPE[4]

5.1. ABSTRACT

Winter is a limiting season for many ungulates in northern, temperate ecosystems, and quality of habitat is an important determinant of winter survival. In Southeast Alaska, Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) are the dominant large herbivore in the coastal temperate rainforest ecosystem, and are strongly influenced by snow depth, which is highly variable within and among years. Widespread timber harvest creates complex landscapes, and the value of forests types likely varies as a function of snow depth. To determine the effect of snow depth on deer selection for vegetation classes, landscape features, and forage biomass, I monitored 56 GPS-radiocollared adult female deer from 1 January to 1 April between 2011-2013. I fit step selection functions using a 2-step approach, with available points defined for each used point based on movement patterns of deer. I found that snow depth had the strongest effect on selection, based on relative effect size. At low snow depths, young second growth was positively selected for and old second growth was avoided, while high-volume old growth was avoided. As snow depths increased, young second growth was avoided and old second growth and high-volume old growth selected. Deer selected strongly for south-facing slopes and increased selection with snow depth, and selected for forb biomass but variably towards other measures of biomass, decreasing selection with snow depth. Deer selection was influenced by availability of vegetation classes and biomass, with positive functional responses for old second growth, productive old growth, and biomass. Deer selection of old second growth decreased with increased availability of productive old growth. Whereas deer displayed plastic patterns of selection with snow depth and availability, behavioral plasticity alone does not ensure animals fulfill energetic requirements if

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adequate forage and snow interception are not available during deep snow events. Therefore, conservation of habitats preferred during deep snow may be critical to ensuring resilient deer populations across variable winters.

5.2. INTRODUCTION

Animals living in seasonal environments must contend with fluctuating resource availability, with survival and population growth often limited by a season in which a limiting resource is scarce (Both et al. 2010; Fretwell 1972; Wolff 1997). For ungulates in ecosystems in temperate zones and higher latitudes winter is often the limiting season for survival, as cold temperatures and snowfall restrict the availability of forage as well as increase the costs of movement (Parker et al. 2009; Messier 1991). In addition, vulnerability of ungulates to predators can be higher in snow-covered landscapes, due to reduced nutritional condition and increased cost of movements for prey relative to predators (Huggard 1993; Nelson & Mech 1986; Sand et al. 2006). Subsequently, spatial selection of ungulates in winter is strongly shaped by the landscapes of energetic cost and risk of death (Gustine et al. 2006).

Ungulates in temperate ecosystems respond to the fluctuating energetic landscape in winter by selecting among habitats that satisfy nutritional needs, reduce cost of locomotion, and potentially to avoid predators. Snowfall interacts with vegetation and landscape structure to determine available forage, cost of movement, and risk of predation. As snow depth increases, values of habitat to wildlife may be completely reversed from low-snow conditions, e.g. as habitat types with abundant forage but little canopy cover to intercept snow become unusable, while habitats with adequate forage and good canopy cover become preferred (Hundertmark et al. 1990). Despite the dynamic, snow-dependent values of habitat to wildlife in winter, most habitat selection studies do not incorporate time-varying snow depth in analyses and model frameworks, instead relying on averaged, winter-long data, or downscaled climate models with large temporal and spatial grain size (but see Fortin et al. 2005; Parker et al. 1996). As a result, winters with consistently deep snow will result in detectable patterns of selection for habitats that reduce snow depth, enhancing forage availability; however, during winters with little snow, selection may be detected for other habitats within the same population

of ungulates (Schoen & Kirchhoff 1985). Moreover, during winters with variable snow depths no strong patterns of selection may be detected at all (Doerr et al. 2005; Yeo and Peek 1992; Person et al. 2009). In areas where snow depth is important for ungulates but expected to be variable within and among years, incorporating frequent measures of snow depth and duration throughout winter likely is key to obtaining accurate measures of habitat preference. Failure to incorporate those data could result in undervaluing important habitats used while snow is deep, and could have negative consequences for management if those habitats are not conserved adequately.

In Southeast Alaska and northern coastal British Columbia, Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) contend with a highly variable winter snowpack, as well as large areas of second-growth forest produced by industrial timber harvest. The value of these forest landscapes to deer depends on the composition of forest patches within various stages of forest succession, climate, and predation regime. Clearcut logging is the dominant method of harvesting timber and young second-growth forests (<30 years post logging) produce abundant forage, whereas older clearcut stands with high levels of light interception by the canopy are typically forage depauperate (Figure 5.1; Alaback 1982). Conversely, the thick canopy of old second growth (>30 years post logging) intercepts most snowfall, whereas there is almost no canopy interception of snow in young second growth (Alaback & Saunders 2013; Kirchhoff & Schoen 1987). Subsequently, forage availability and cost of movement in second-growth stands depends strongly on snowfall, and the value of timber-harvested landscapes to ungulates and other wildlife will vary across regions, climate cycles, and within and across years as dictated by snowfall.

Deer in the coastal temperate rainforest of Southeast Alaska and British Columbia present an excellent study system to examine the interactive, time-dependent effects of industrial timber harvest and snow on temperate ungulates. In Southeast Alaska, commercial clearcutting of timber is widespread and focused on old-growth forest, creating major shifts in habitat (Alaback 1982; Alaback & Saunders 2013; Hanley & Brady 1997). In winter, deer rely on evergreen forb species and twigs of woody shrubs for food (Parker et al. 1999), which are typically available in old-growth forest types but not in old second growth (Hanley et al. 2012). Energy intake is lower than energy

expenditure and variability of expenditures generally determines energy balance more than variability of intake (Parker et al. 1996). Some previous studies showed that in winters with significant snow persisting throughout the winter, deer strongly selected for habitats in which snow was minimal yet some understory forage was available, particularly old-growth forest on south-facing slopes (Schoen & Kirchhoff 1985, Kirchhoff & Schoen 1987). Several other studies indicated that selection for those habitats was weaker during winters with more intermittent snowfall and duration (Person et al. 2009; Doerr et al. 2005; Yeo & Peek 1992). However, all of these studies considered snow depth based on annual averaged values, whereas deer undoubtedly respond to changing snow depth at much finer temporal and spatial scales (Parker et al. 1999).

Here, I examine the effects of snow depth on selection of movements relative to vegetation classes, forage biomass, and landscape features by Sitka black-tailed deer. I hypothesized that as snow depth increased, deer would increasingly select locations with more canopy interception, but that locations that provided both canopy interception and forage would be preferred. I test predictions at the scale of deer movements, as snow depth strongly affects cost of movement and deer home ranges are greatly restricted in winter compared to summer (Schoen & Kirchhoff 1985; Yeo & Peek 1992). Deer may also respond behaviorally to the availability of habitats, particularly if some habitats are of higher value than others but availability of high-quality habitats is limited (Knopff et al. 2014; Moreau et al. 2012), or potentially if animals prefer abundant habitats compared to rarer habitats of the same quality. In the context of timber management, when animals do not have sufficient old-growth habitat available to fulfill biological requirements, second-growth habitats likely will be used. As a result, I expect a functional response in selection of second growth, with a positive relationship between selection of second-growth forests and availability of second growth to the animal, and a negative relationship between selection of second-growth forests and the availability of high-quality old-growth forest types. Conversely, if there is little of a particular old-growth forest type available (i.e., rare or patchily distributed within the home range), deer may not use that habitat type when there is significant snowfall because cost of movement to

reach a patch of that type would be high (i.e., snow reduces connectivity). Instead, deer may select more common forest types with greater continuity.

5.3. METHODS

5.3.1. Study Area

This study was carried out on the central portion of Prince of Wales Island, the largest island in the Alexander Archipelago of Southeast Alaska and the third largest in the United States (Figure 2). The ecosystem is coastal temperate rainforest, with natural habitats spanning a variety of old-growth forest types, as well as muskeg heaths, wet meadows, estuaries, beaches and shorelines, and numerous lakes and rivers. In addition, since 1954, Prince of Wales has been the focus of much of the commercial timber harvest in the region (Albert & Schoen 2013), which created extensive even-aged stands that are of varying successional stages and value to wildlife (Alaback 1982; Hanley et al. 2005). Much of the land area in Southeast Alaska, including the entirety of the study area, was part of the Tongass National Forest, the largest National Forest in the United States. Annual precipitation is in excess of 300 cm per year in many areas, with average winter snowfall varying across the region (Shanley et al. 2015). In the study area on Prince of Wales, snow levels are relatively low in comparison with areas of the archipelago that are farther north. However, heavy snowfall can occur and persist, and deer populations decline sharply in response (Brinkman et al. 2011).

There are multiple sources of mortality for deer in the study area, primarily human hunters, malnutrition, and predation by wolves (*Canis lupus*) and black bears (*Ursus americanus*) (Person et al. 2009). Wolf densities are currently quite low on Prince of Wales Island (Alaska Department of Fish and Game 2014), and I observed no predation of adult female deer marked during the study. However, Sitka black-tailed deer exhibit anti-predator behavior in response to wolf sign even after 100 years of absence, indicating that avoidance of wolf predation risk is likely to continue to drive deer behavior (Chamaillé-Jammes et al. 2014). Bear predation is absent during winter months while bears hibernate, and hunting season close in December. Malnutrition was the major cause of death for adult female deer during winter over the course of this study.

5.3.2. Deer Capture and GPS Monitoring

I captured 63 adult female deer between 2010 and 2012, following procedures described in Gilbert et al. 2014. All captures were carried out in accordance with approval of the University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC #136040-14). Each deer was fitted with a GPS tracking radio collar (Telonics, Isanti, MN) that recorded locations every 2 hours for one year. For this winter-focused analysis, I considered relocations only between January 1 and April 1 of each year. Consequently, 6 deer that died before winter were not included in this analysis.

5.3.3. Spatial Covariates

I considered vegetation classes, topography, landscape variables, and forage variables in spatial analyses (Table 5.1). In addition, I considered possible interactions between those covariates and daily snow depth across the landscape. Vegetation classes were derived from the community types developed by the Forage Resource Evaluation System for Habitat (FRESH; Hanley et al. 2014) model for deer in Southeast Alaska, created by the U.S. Forest Service and described in detail by Hanley et al. (2012). However, I combined a number of community types to reduce the numbers of classes for spatial analyses, and considered a reduced set of vegetation classes (Table 1) thought to be important in winter. Resulting vegetation classes included old-growth and second - growth forest types, as well as a number of other naturally occurring vegetation classes.

Available forage depends on the height of plants, the snow depth at plant locations, and the resistance of plants to burial (i.e., plants bending under the weight of snow). Although there are several equations available relating snow depth to forage burial (Hanley et al. 2012; White et al. 2009), I did not explicitly examine forage burial by snow, rather I inferred levels of snow interception, snow accumulation, and duration of burial for vegetation classes by 1) using canopy interception of vegetation classes to modify daily snow depth maps used in deer models, and 2) allowing snow depth to modify deer selection for forage variables by fitting snow by forage interactions within deer selection models. I used the FRESH model values for forage biomass in each community type to create spatial maps of total biomass, shrub biomass, and forb biomass, as well as to produce a spatial map of canopy interception across the landscape.

5.3.4. Snow Record

Snow levels are highly variable across the Southeast Alaska landscape, with effects of elevation, aspect, slope, and canopy cover. In addition, weather stations are sparsely distributed across the landscape (Simpson et al. 2005), making projections of snow depth to specific locations such as deer GPS relocations difficult. Subsequently, I deployed snow stations across the study area to more accurately characterize variability experienced by deer. I deployed 23 stations, each consisting of a vertical stake with an array of 3 pendant-style temperature loggers (Hobo tidbit loggers, Onset Computer Corporation, Bourne, MA) attached at 10 cm, 25 cm, and 50 cm above ground level, along with another pendant logger encased in a solar radiation shield (Ambient Weather, Chandler, AZ) to measure air temperature (Lewkowicz 2008). I chose Hobo loggers because of the high precision of temperature data collected (± 1 C°), given that winter air temperatures in the study region often hover near freezing in winter (Simpson et al. 2005). Stations were placed in open, flat muskegs or meadows, and at least 25m from forest edges in order to avoid potential edge effects on snow depth. Temperatures were recorded every 3 hours throughout the year, and data were downloaded once per year.

To detect snow from recorded temperatures at snow stations, I used several filtering criteria to translate patterns in temperature across the array of temperature loggers into snow coverage for each logger in the arrays. For each station, I constructed 24-hour moving window values for mean and standard deviation of temperature of the air logger, and mean and standard deviation of the temperature of the temperature loggers. The filtering criteria applied to these data included: a) the temperature differential between means of air and temperature loggers (i.e., differences > 1 C°); and b) the mean and standard deviation of the temperature logger (i.e., mean $\leq$ 1.4 C° and SD $\leq$ 0.55 C°). I validated these thresholds using the period of 6-24 January 2012, when snow depth was recorded manually once per day during field visits to 10 stations. I used a range of filtering values, and chose final filtering values based on classification success (i.e., snow-covered or non-covered in the validation data set). The resulting data, reflecting whether the 10-cm, 25-cm, and 50-cm temperature loggers at each station were covered

with snow or not, were then translated into minimum snow depths of 0.10, 0.25, or 0.50 m at each station every 3 hours.

Daily median snow coverage was then calculated at each station. These daily snow level data were corrected for elevation to produce sea level snow equivalents (cm), using an equation relating elevation to snow depth developed in Juneau, AK (Hanley et al. 2012). These corrected daily snow levels for each station were interpolated across the extent of the study area using inverse distance weighting among stations using gstat package (Pebesma 2004) in program R (R Development Core Team 2014). Subsequently, the raster layer of daily snow depth at sea level was modified by elevation (m), slope (degrees), aspect (degrees), and canopy cover (%), using linear relationships developed in Southeast Alaska and described in detail in FRESH (Hanley et al. 2012).

5.3.5. Deer Habitat Selection

I considered deer habitat selection at the scale of deer movements, as deer in winter in the study area are presumably strongly affected by the cost of movement through deep snow, which constrains both use and availability of locations. I used step selection functions (SSF, Fortin et al. 2005), which compare covariates of used and potentially used (i.e., available) locations or step segments between locations. SSFs share much in common with the more familiar resource selection functions (RSFs; Johnson et al. 2006), but use movement patterns to generate random available steps for each used step. SSFs can compare either line segments between locations (i.e., steps), or the endpoints of segments (i.e., locations) to steps or locations that could have been chosen at that time-step. By using movement patterns to define the set of available steps or locations, the definition of availability is refined and may result in better models of actual selection by animals (Thurfjell et al. 2014). Once matched sets (i.e., strata) of used and available steps are generated for each individual (i.e., cluster), use and availability are compared using conditional logistic regression, taking the same generalized linear form as an RSF with a log link function:

$$\widehat{w}(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n) \qquad (1)$$

Where β_n are coefficients estimated by conditional logistic regression, and associated with covariates x_n, and $\widehat{w}(x)$ represents the relative probability of a step or location being selected by an individual deer (Fortin et al. 2005). I chose to analyze used and available locations rather than steps between locations, as deer likely make circuitous movements between the 2-hour fixes, particularly with increasing snow depth. I generated 5 available points per used point using matched, randomly chosen turning angles and step lengths, drawn from distributions based on the combined movements of all deer in the study. Because relocations of individual deer are serially correlated, I analyzed selection with a 2-step approach, estimating parameters at the individual, then the population level using the TwoStepCLogit package in program R. This allowed us to examine potential functional responses in selection of individuals relative to timber-harvested vegetation classes as a function of the availability of timber-harvested and old-growth classes, and to selection of biomass relative to availability of biomass.

Candidate models were developed within 3 covariate groups: vegetation classes, landscape covariates, and forage biomass covariates. Within the vegetation class variables, I divided covariates into old-growth and second-growth forest models, and subdivided female data so that each female included had all old-growth or second-growth classes available to them. As a result, forage model sets included 56 female deer, landscape model sets included 54 deer, old-growth model sets included 32 deer and second-growth models sets included 14 deer. I considered all subsets of covariates within covariate groups, as well as versions of each model that included interactive effects of snow with each covariate; for the forage group, this resulted in 6 forage models, 14 old-growth models, 6 second-growth models, and 14 landscape models. In addition, I did not include highly correlated covariates ($|r| > 0.6$) in the same models.

I used a two-step modeling approach, as described by Fieberg et al. (2010). While mixed-effects models with random effects of individuals are commonly used to control for autocorrelation within individuals' data, such models become complex and difficult to fit when random effects for each spatial covariate are included, and conditional logistic regression with conditioning on each relocation cluster is used (i.e., available point clusters conditional on each used point; Fieburg at al. 2010). I fit all models within each covariate group to each individual deer. Within each group of models, I calculated AIC

values and weights (Burnham & Anderson 2002) for each individual model, and an average AIC weight for each model structure across individuals. I report top-ranked sets of models within each covariate group with an average AIC weight of at least 0.1. To estimate coefficients and standard errors at the population level, I averaged coefficient values from each top-ranked model within each group, using the TwoStepCLogit package (Craiu et al. 2011) in program R. In addition, I calculated the relative effect (RE) size (Riggs and Pollock 1992) for each covariate in the top-ranked model by changing each covariate by 10% (e.g., an RE of 1.5 indicates a 50% increase in the probability of selection for a 10% increase in a covariate). I calculate 85% confidence intervals around estimates of RE, as this has been suggested as a more appropriate value for use in conjunction with AIC-based model selection (Arnold 2010).

I evaluated patterns in variation of selection patterns among individual deer, testing for functional responses in selection of second-growth classes dependent on availability of second growth, selection of old growth in response to availability of old growth, and selection of forage biomass in response to availability of biomass. In addition, I examined whether deer selection of second growth was influenced by availability of old-growth alternatives. I compared individual coefficients of selection to mean values of available points for each individual (Knopff et al. 2014; Moreau et al. 2012). For these analyses, I used the individual deer coefficients for variables from the best-ranked model in which that coefficient appeared.

I expected positive relationships between availability of all second-growth classes and selection for each second-growth class, and negative relationships between availability of alternative old growth and selection of second growth (i.e., if low- and medium-volume old growth was more available, selection of young second growth should decline, and if medium- and high-volume old growth was more available, selection of old second growth should decline). Additionally, I expected increased selection of old-growth classes when they were more available, and decreased selection for forage covariates when more forage was available. I tested for associations between coefficients and availability using rank-based correlation tests (i.e., Kendall's tau), as some distributions of availability of covariates across individuals were not normally distributed and sample sizes (i.e., numbers of individuals) were low. Only correlations

with $p < 0.05$ are reported as demonstrating an association, although given the low sample size, this may exclude some real associations.

5.4. RESULTS

5.4.1. Patterns in Snow Depth and Temperature

Snow stations with temperature loggers proved to be effective tools for measuring snow depth, although a number of stations were damaged by bears during summer months and loggers subsequently had to be replaced. There was considerable variation in snowfall within and across the 3 winters included in the study, and among deer home ranges (Figure 5.3 a). Median snow depth across winter home ranges of deer in the study for the 90 days of the study was 0.25 m (Median absolute deviation (MAD) = 0.10 m) in 2011, 0.33 m (MAD = 0.08 m) in 2012, and 0.23 m (MAD = 0.01 m) in 2013. Correcting daily snow maps to a universal 100 m elevation, median snow depth across the study area (i.e., central Prince of Wales Island) was 0.13 m (MAD = 0.13) in 2011, 0.17 m (MAD = 0.10) in 2012, and 0.13 m (MAD = 0) in 2013. Snow depths were far more variable in 2011 and 2012 than in 2013. Based on the 100-m elevation corrected maps, median snow depths at 100 m elevation in the study area exceeded 0.25 m for a cumulative total of 21 days in 2011, 25 days in 2012, and 12 days in 2013 (Figure 5.3 b).

5.4.2. Deer Habitat Selection

Deer selection varied across old-growth and second-growth forest types, as well as by landscape and forage variables. Interactive effects with snow depth were supported for many of these covariates (Table 5.2). In addition, the top-ranked model within each covariate group of models based on AIC weights included interactive effects of snow for all covariate in the models (Table 5.2). Across all models, deer selected against snow depth, which was the most influential variable based on relative effect size (Table 5.3). Indeed, a 10% increase in snow depth equated to a decrease in probability of selection of 20-40%, depending on which estimate of the snow coefficient was used (Table 5.3).

Because sample sizes differed across model groups due to some individual deer not having all covariates available to them, AIC scores could be compared within but not among groups. However, relative effect (RE) size does provide a way to compare relative

importance of covariates across groups. Across top-ranked models in the forage group (Table 5.2), deer selection was highly variable and negative for total biomass (β = -0.12 , SE = 0.32) and shrub biomass (β = -0.07, SE = 0.54), and decreased as snow depths increased in a resource unit (β = -0.94, SE = 0.65 for total biomass, β = -0.67, SE = 0.43 for shrub biomass). Selection was positive and variable for forb biomass (β = 0.20, SE = 0.48), but also decreased with increasing snow depth in a resource unit (β = -0.64, SE = 0.90). Model AICc weights were almost equal for the top three models in the forage group, indicating that there was support for the effects of all three measures of forage biomass (Table 5.2). Total forage biomass, the measure of forage in the top-ranked model in the forage group, had a small relative effect size of 0.99 (85% CI = 0.94, 1.04; Table 5.3), indicating that a 10% increase in total biomass produced a 1% decline in probability of selection by deer. However, an 18-cm (10%) increase in snow depth within a resource unit equated to a 3% decrease in selection for total biomass (RE = 0.93, 85% CI = 0.87, 0.99). Much of the variability among individual deer in selection for measures of forage appeared to be explained by a positive functional response by deer to availability of forage, indicating that when forage was abundant among available resource units, deer were more likely to select for it, but when it was rare, deer did not select for high-forage resource units (Figure 5.4b). Strength of these associations, based on Kendall's rank correlation tests between availability and selection, yielded values of r = 0.37 ($p < 0.001$) for total forage biomass, r = 0.40 ($p < 0.001$) for shrub biomass, and r = 0.39 ($p < 0.001$) for forb biomass.

Among the landscape group of models, the top-ranked model set comprised four models, and the best-supported model (AIC weight = 0.21) included effects of edge density, road density, southing, and interactive effects of snow with these variables. Landscape covariates had contrasting effects on deer probability of selection. In general, deer selected resource units with lower road (β = -0.02, SE = 0.01), and edge density (β = -0.01, SE = 0.01), but probability of selection of roads and edges for movement increased as snow depth increased (β = 0.02, SE = 0.02, and β = 0.03, SE =0.02, respectively; Table 5.2). In contrast, selection of south-facing slopes was positive (β = 0.002, SE = 0.002), and deer increased selection for south-facing slopes as snow depths within a resource unit increased (β = 0.007, SE = 0.003). Landscape covariates had relatively large relative

effect sizes, which we report here with 85% confidence intervals (CI); notably a 10% increase in southing (18 degrees) at a location was 6% more likely to be selected (85% CI = 0%, 8%), and a location with mean southing and 10% more snow (18 cm) was 14% (85% CI = 6%, 22%) more likely to be selected (Table 5.3).

Deer selection relative to old-growth forest types was influenced by snow depth (Figure 5.5), and the best-supported model (AIC weight = 0.28) included all three old-growth forest types and interactive effects with snow (Table 5.2). Deer avoided high-volume old-growth forest (β = -0.45, SE = 0.34), and had highly variable responses to medium-volume forest (β = 0.09, SE = 0.36) and low-volume forest (β = 0.09, SE = 0.30) at low snow depth. As snow depth at a resource unit increased, deer increasingly selected for high- and medium-volume forests (β = 0.91, SE = 0.34 and β = 0.21, SE = 0.73, respectively; Figure 5.5), while deer selection for low-volume forest varied widely (β = 0.004, SE = 0.58). This considerable variation among individuals was in part explained by functional responses to availability of old-growth forest types; when old-growth forest types were common among available resource units, deer were more likely to select those old-growth types (i.e., a positive functional response; Figure 5.4). Kendall's rank correlation tests indicated that two of these positive relationships were significant, with r = 0.28 (p = 0.007) for low-volume old growth, and r = 0.31 (p = 0.003) for medium-volume old growth. As a result of the high levels of variability in selection among individuals, mean relative effect sizes were low for old-growth types (Table 5.3), but 85% CIs reflect the larger range of effect sizes for individual deer.

Deer selection towards second-growth vegetation classes was highly variable, and the best-supported model (AIC weight = 0.48) included effects of young and old second-growth forest and interactive effects with snow (Table 5.2). On average, deer selected positively for young second growth (β = 0.62, SE = 0.41), and negatively for old second growth (β = -0.25, SE = 0.41), although there was large variation among individuals with respect to selection against old second growth (Figure 5.6). The relative effect size for young second growth was large: a location with 10% more young second growth within a 100-m buffer was 6% (85% CI = 0%, 13%) more likely to be selected. In contrast, a location with 10% more old second growth was 2% (85% CI = -4%, 8%) less likely to be selected. As snow depth increased, deer increasingly avoided young second growth (β = -

0.25, $SE = 0.91$) but increasingly selected for old second growth ($\beta = 0.66$, $SE = 1.20$; Figure 5.4). A 10% increase in snow depth for a resource unit with average values of young second growth equated to a 1% decrease in probability of selection, whereas for a resource unit with average values of old second growth, the same increase in snow resulted in a 2% increase in probability of selection (Table 5.3). There was a positive relation between strength of selection of second-growth classes and the proportion of matching available points that were located in that class (Figure 5.5). For example, as availability of old second growth increased, deer selected more strongly for old second growth (Kendall's rank correlation test, r = 0.40, $p = 0.03$). In addition, there was some evidence that deer were less likely to select for second-growth forest when productive old-growth forest types were more available (Figure 5.5), however only the correlation between selection of old second growth and availability of medium-volume old growth was significant with $p < 0.05$ (Kendall's rank correlation test, r = -0.43, $p = 0.02$).

5.5. DISCUSSION

Deer movements in winter were strongly affected by snow depth, and snow depth determined the direction and magnitude of selection for vegetation, forage, and landscape covariates. Selection was highly variable among individuals, and deer increasingly used second-growth forests as availability of second growth increased, and availability of old growth decreased. Selection of each old-growth forest type also increased with the availability of that old-growth type. Surprisingly, shrub and total forage biomass were not good predictors of deer selection of movements in winter, although forb biomass was; rather, deer simply select resource units that were locally abundant and had sufficient forage and snow interception, rather than seeking out the locations with greatest availability of forage. Deer had short average step lengths between relocations (median = 48.21 m, median absolute deviation = 51 m), and as a result, availability for selection of consecutive movements was defined quite locally. This could explain the positive relationship I observed between availability of old-growth habitat types and selection of those types, with deer selecting locally abundant old growth and avoiding isolated patches of old growth far from other patches. In the winter landscape, with cost of movement potentially high, selection of distant, isolated patches carries risks, as deer can

become stranded by further snowfall in an old-growth "island" with dwindling forage (Kirchhoff 1994). As snow depth increased, deer moved out of young second growth and into productive old-growth forests (i.e., medium- and high-volume strata), and appeared to choose old-growth forest types that were widely available, and presumably less isolated.

Interpreting snow interactions is complex. Forest canopy, elevation, slope, and aspect of a location were part of the snow depth calculations I used, so that snow depth in the models is a measure of snow depth in that habitat, rather than snow depth in an adjacent open habitat. For instance, deer increasingly selected medium- and high-volume old-growth forest types as realized snow depth at that location increased, yet nearby available patches likely had even higher levels of snow, as reflected by negative selection relative to snow depth itself. Likewise, deer selection of south-facing slopes increased dramatically with increased snow depth, as south-facing slopes generally have lower snow than other aspects (Hanley et al. 2012). The increased levels of selection for edge and road density as snow depth increased likely reflect higher forage and lower snow in these areas, but there were not sufficient data to include these effects in modeling efforts.

Our results indicate that the timing and distribution of timber harvest matters to deer movement and thus to winter connectivity. If large proportions of habitat relative to deer home range size are clearcut, or if remaining old growth is primarily low-volume, unproductive forest, deer will not be able to move into productive old-growth types as snow depth increases. Additionally, if high-quality, high-volume old growth is preserved but is patchily distributed, deer appear to be less likely to select it. Although deer increased selection for old second growth as snow depth increased, and were more likely to use old second growth as it was increasingly available, old second-growth stands have very low forage available to deer. Deer may use old second growth as a matrix through which to move at high snow depths, and if productive old growth is not available, but energy budgets of these individuals will likely be negatively affected if productive old growth is not available.

Young second-growth cuts are considered to be returned to productivity for deer after 15 years, and neighboring stands of old-growth forest can then be cut under current Tongass Forest Service regulations (U.S. Forest Service 2008). Negative consequences of

this strategy may not manifest in low-snow winters, when deer can successfully subsist in young second-growth landscapes, but will likely appear in deep-snow winters, when deer are forced into isolated remaining old growth or into the increasingly abundant old second growth. Restoration of deer forage within old second growth using small selectively cut patches has been proposed, wherein forage regenerates within and along the edges of clearings and is partially available during winter due to edge effects (Alaback 2010). However, there are no data for deer use of such treatments and their value is purely speculative. Further research into the design of such treatments and the preferences of deer across designs is crucial for maintaining deer populations through harsh winters in landscapes dominated by even-aged timber harvest.

Although these results improve our understanding of deer habitat requirements in winter, an important next step will be to link habitat use to fitness outcomes. Farmer et al. (2006) documented that while yearling and adult female deer selected young second growth, their risk of death from hunting and wolf predation is increased with increased use of this habitat. Snow depth could interact with habitat use to alter risk of predation, for example if deer are more vulnerable to wolf predation when concentrated in certain habitats during deep snow. In addition, I did not include predation risk as a predictor in deer selection models, although wolves are present on the island and prey on adult female deer in winter. Exploration of the role of predation risk in driving deer selection in winter is important, as predation risk can render otherwise high-quality winter habitat effectively inaccessible to deer (Kauffman et al. 2014). Another promising direction for future investigation is the fitness consequences of winter habitat use by fawns, which likely select habitat similarly to adult females but are under greater nutritional strain due to lower body reserves (Parker et al. 1999), shorter leg length (Parker et al. 1984), and a higher critical thermal temperature (Parker 1988).

A shortfall of this analysis is that I analyze habitat selection at a single spatial scale. Deer likely select at multiple scales (Kie et al. 2002), and selection of seasonal (winter) home ranges at the landscape is likely to be important in determining deer survival as well (Decesare et al. 2013). For example, Farmer et al. (2006) found that landscape variables within 500-m buffers best explained survival patterns in yearling and adult females. Analysis of winter selection within the annual home range is an important

next step, and could be integrated with the results of this work to produce multi-scale predictions of deer selection at differing snow depths. Such an approach could be an important tool for modeling deer habitat suitability under future climate change scenarios, which predict much reduced average snow depth for Southeast Alaska but increased storm frequency (Cherry et al. 2010; Shanley et al. 2015).

Our findings expand on several previous studies, explaining several contradictory findings among studies and contradicting some past findings. The importance of productive old growth to deer in Southeast Alaska is generally accepted, however, various studies reached different conclusions as to its relative importance compared to other factors. On Admiralty Island, where deep snow is common, Schoen and Kirchhoff (1985) documented strong selection by radio-collared deer for productive old-growth forest during winter. In contrast, studies on Prince of Wales (Yeo & Peek 1992) and Mitkoff Islands (Doerr et al. 2005), where average snow levels are lower and intensive logging is widespread, found that south-facing slopes were more important than productive old-growth for winter habitat, which deer were neutral to or avoided. Finally, a recent meta-analysis of VHF-based deer selection (Person et al. 2009) detected weak selection for productive old growth in deep snow winters, and an increased selection for productive old growth on south-facing slopes. My results clarify these apparently conflicting lines of evidence, as I found that deer avoided productive old growth at low snow depths, but increased selection for productive old growth as snow depth increased. As documented by these prior studies, I also detected strong selection by deer for south-facing slopes, which I found to be greatly amplified by snow depth.

The potential for second-growth forests to provide habitat for deer in winter is not well understood, although snow depth is thought to play an important role in determining the value of young second growth to deer. Yeo and Peek (1992) and Doerr et al. (2005) documented selection by deer for young second growth during snow-free months, and general avoidance of old second growth. The results of this study shed further light on the use of second-growth forests by deer in winter, confirming that deer select for young second growth at low snow levels but increasingly avoid it as snow accumulates. In addition, old second growth was avoided at low snow depths, but increasingly selected as snow accumulated, indicating that this habitat, which intercepts snow well, could play an

important role in providing connectivity between old-growth forest patches during deep-snow conditions.

Snow depth had by far the largest effect of any variable in the models. As Parker et al. (1999) found, deer appeared to select habitat to optimize the trade-off between energy gains of forage with energy expenditures of movements. Forb biomass was selected, while selection towards shrub biomass was mixed, and selection for all measures of biomass decreased with increasing snow depth at a location. Person et al. (2009) found that elevation, slope, and aspect were the most influential determinants of selection by deer during winters with snow. Although Person et al. (2009) did not measure variability of snow through time and space, these covariates are the primary determinants of snow accumulation across the landscape (Hanley et al. 2012; Shanley et al. 2015), and I used these covariates to create daily snow maps used in deer models.

The frequent, high-resolution measurement of snow depth in this study, combined with GPS radiotelemetry, allowed us to improve on and reconcile the results of past studies, which were based on VHF radio-collared animals, pellet surveys, or direct observations of individuals (with correspondingly low sample sizes). As a result, it is not surprising that the high-intensity sampling of individuals via GPS relocation, combined with frequent automated measurements of snow depth, produced a more nuanced picture of deer selection in winter that is dynamic, flexible, and highly dependent on snow depth.

The strong influence of snow on selection by deer, including the reversal of selection direction towards young second growth and high-volume old growth, indicate that the winter landscape is highly variable in its value for deer dependent on snow depth. Deer respond flexibly to increasing snow depth, avoiding deeper snow, choosing locations with higher levels of forb biomass, adapting to exploiting young second growth at low snow levels when it is increasingly available, and using old second growth when productive old growth is less available. This plasticity of selection is important for deer in Southeast Alaska, where timber harvest creates a diverse matrix of altered and unaltered landscapes. However, behavioral plasticity is unlikely to fully compensate for inadequate forage or snow interception, making careful consideration of timber harvest configuration and rotation important considerations for managers.

5.6. ACKNOWLEDGEMENTS

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5.7. FIGURES

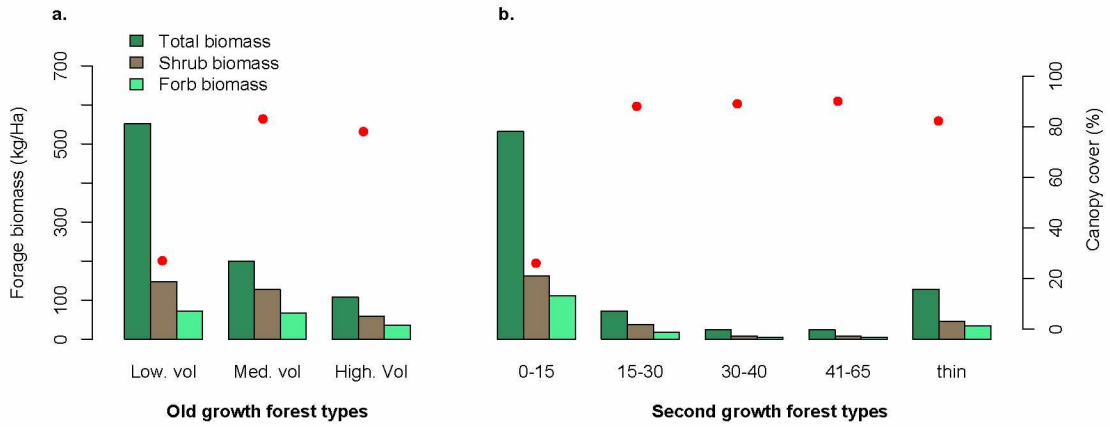

Figure 5.1. Forage and Canopy Differences Among Vegetation Classes

Differences in winter forage biomass (total, shrubs, and forbs, in kg/Ha) among **a)** old-growth forest types, from low-volume to high-volume types, and **b)** second-growth forest types, from 0-65 years after original timber harvest, and when pre-commercial thinning has taken place. Red dots indicate percent of canopy cover. Values are derived from the FRESH forage model community types.

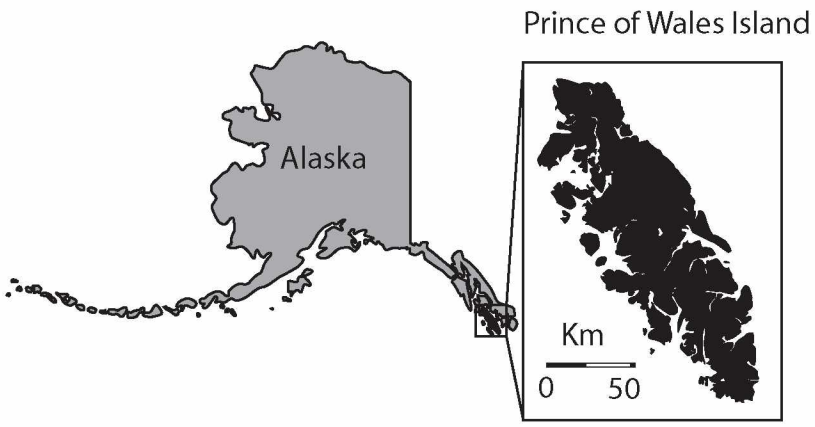

Figure 5.2. Study Area Map

The study area was located on the central portion of Prince of Wales Island, in the Alexander Archipelago of Southeast Alaska.

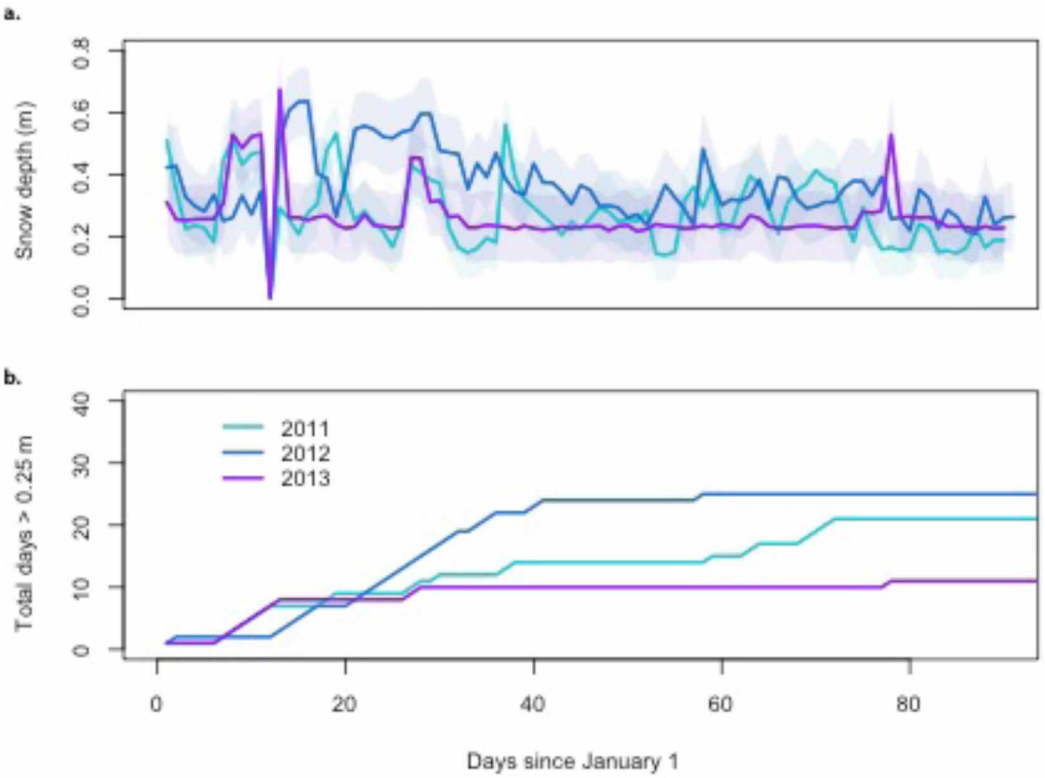

Figure 5.3. Variability in Snow Depth Within and Across the Years of the Study Shown are **a)** daily mean and 95% CIs for snow depths (m) across winter home ranges for female deer monitored from January 1 – April 1 during 2011, 2012, and 2013, and **b)** cumulative number of days at 100-m elevation with greater than 0.25m snow depth for the same period each year.

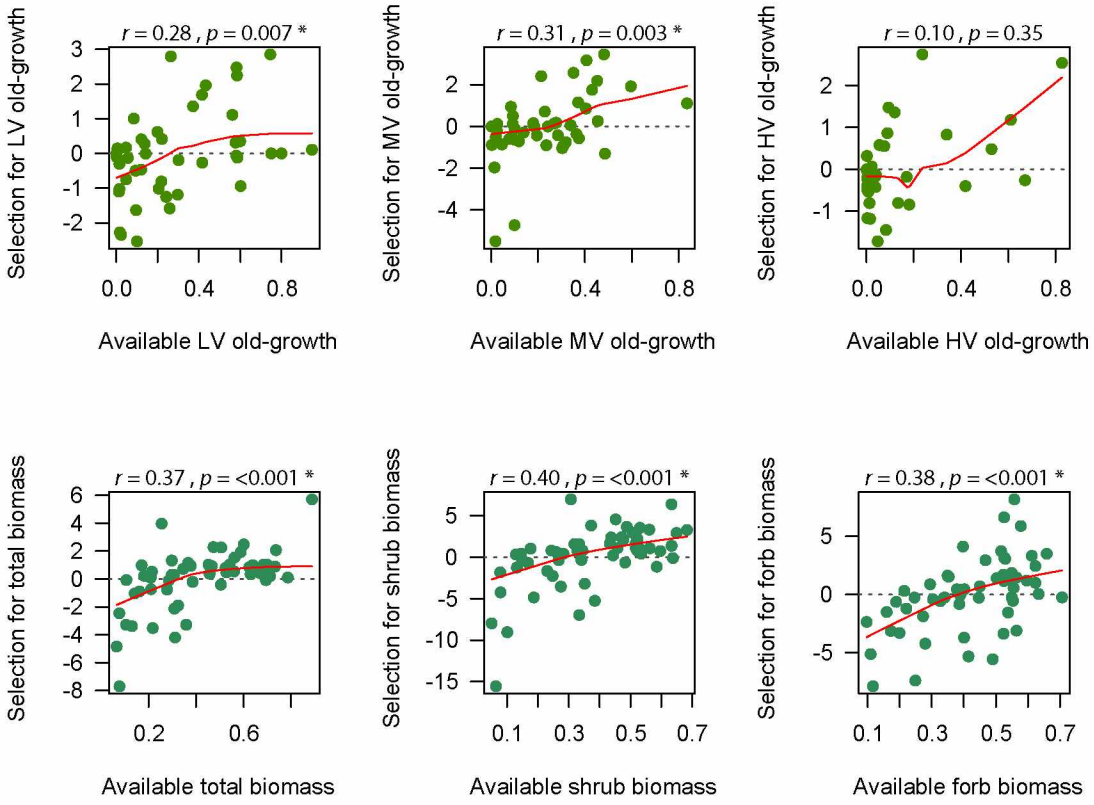

Figure 5.4. Deer Functional Responses to Old-Growth Forest Types and Forage Biomass
Shown is variation among individuals in selection of old-growth forest types and biomass measures as functions of availability.

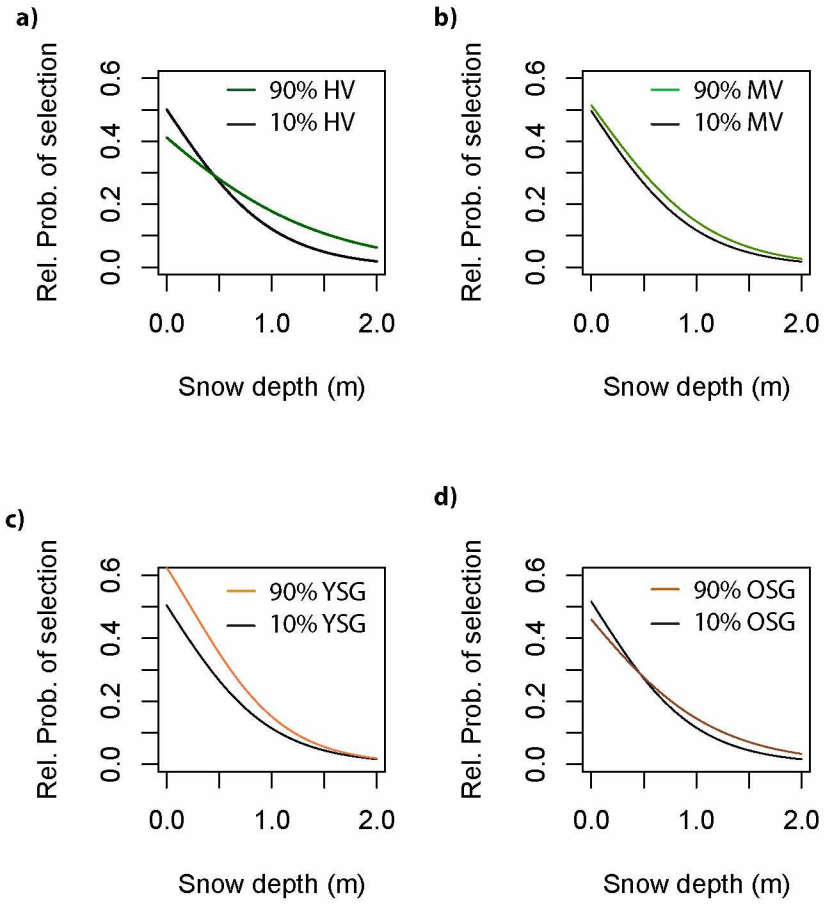

Figure 5.5. Interaction of Snow Depth and Deer Selection Responses to Forest Types Probability of selection depends on snow depth and forest type, with probability of selection for a) high-volume (HV) old-growth forest increasing, b) medium-volume old-growth forest (MV) increasing, c) young second-growth forest (YSG) decreasing, and d) old second-growth forest (OSG) increasing with increasing snow depth.

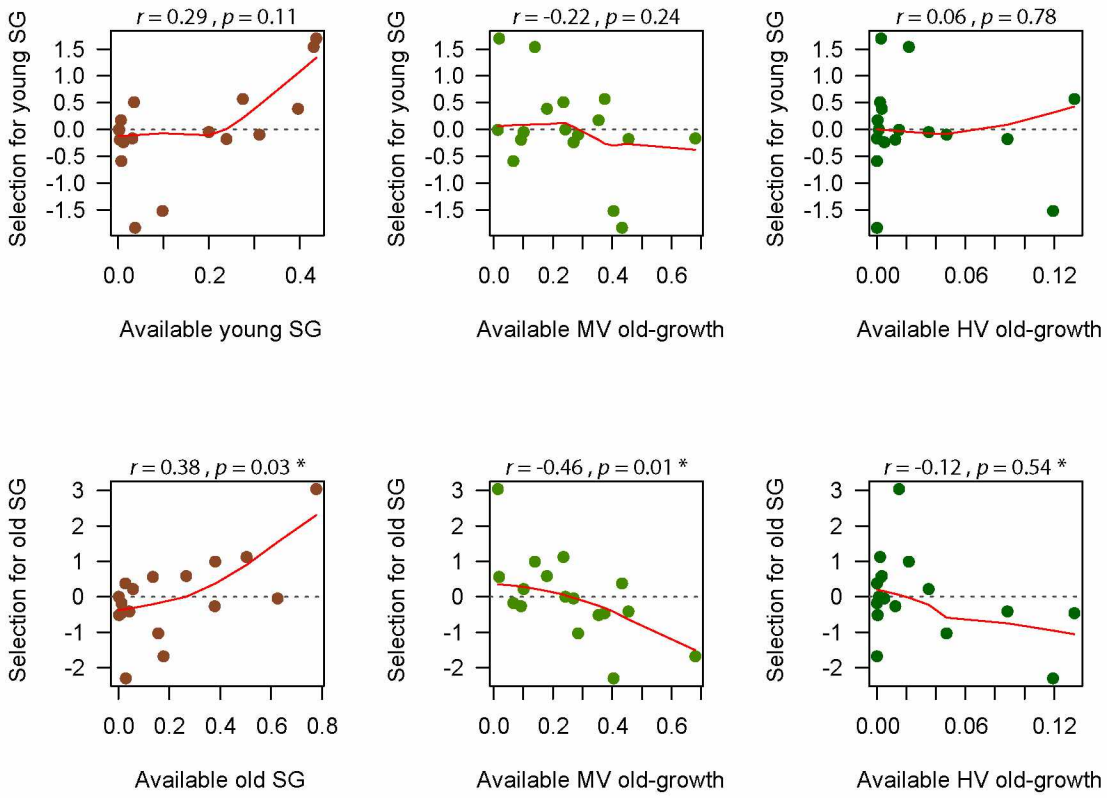

Figure 5.6. Deer Selection Responses to Second-Growth Forest Types

Shown is variation among individuals in selection of second-growth forest types as functions of availability of second-growth (i.e., functional response), and as functions of availability of alternative, productive old-growth forest types.

5.8. TABLES

Table 5.1. Variable Types and Descriptions Used in Spatial Analysis

List of spatial covariates by group used in models of adult female deer spatial selection in winter.

Variable group Variable	**Description**
Vegetation class	Proportion of vegetation classes[a] within moving windows[b]
Low-volume old growth	Intact forest classified by USFS as unproductive
Medium-volume old growth	Intact forest classified by USFS as size density 4 or 5
High-volume old growth	Intact forest classified by USFS as size density 6 or 7
Young second growth	Clearcut forests, 0-30 years after harvest
Old second growth	Clearcut forests, >31 years after harvest
Landscape Characteristics	
Southing	Average degrees that face south (0=100% north facing, 180=100% south facing) within moving windows.
Edge density	Density of edges within moving windows
Road density	Density of roads within moving windows
Forage Characteristics	
Total biomass	Total biomass of forage plants in winter (kg/km^2) within moving windows
Forb biomass	Biomass of forbs in winter (kg/km^2) within moving windows
Shrub biomass	Biomass of shrubs in winter (kg/km^2) within moving windows

Table 5.2. Coefficients for Top-Ranked Models of Deer Selection

Interactive effects with snow depth are indicated with the * symbol. Only models with a mean AIC weight (*w*AIC) > 0.10 are reported for each covariate group of models.

Variable	**Rank 1 model** *β (SE)*	**Rank 2 model** *β (SE)*	**Rank 3 model** *β (SE)*	**Rank 4 model** *β (SE)*
Forage models				
Total biomass	-0.02 (0.05)	--	--	--
Total bio*snow	-0.16 (0.10)	--	--	--
Shrub biomass	--	--	-0.03 (0.20)	-0.12 (0.15)
Shrub bio*snow	--	--	-0.67 (0.43)	--
Forb biomass	--	0.14 (0.37)	--	--
Forb biomass*snow	--	-0.64 (0.90)	--	--
Snow depth	-1.27 (0.91)	-1.91 (1.07)	-1.10 (0.99)	--
*w*AIC	0.26	0.23	0.22	0.12
Landscape models				
Edge density	-0.01 (0.01)	-0.01 (0.01)	-0.01 (0.01)	--
Edge density*snow	0.03 (0.02)	--	0.03 (0.02)	--
Road density	-0.02 (0.01)	-0.02 (0.01)	--	-0.03 (0.01)
Road density*snow	0.02 (0.02)	--	--	0.01 (0.02)
Southing	0.002 (0.002)	0.004 (0.001)	0.002 (0.002)	0.003 (0.002)
Southing*snow	0.007 (0.003)	--	0.008 (0.003)	0.005 (0.003)
Snow depth	-2.38 (0.70)	--	-2.18 (0.68)	-2.09 (0.68)
*w*AIC	0.21	0.16	0.12	0.11
Old-growth vegetation models				
Low volume OG	0.09 (0.30)	-0.04 (0.31)	-0.22 (0.18)	--
Low vol. OG*snow	0.004 (0.58)	--	0.12 (0.35)	--
Med. volume OG	0.09 (0.36)	0.14 (0.36)	--	--
Med. vol. OG*snow	0.21 (0.73)	--	--	--
High volume OG	-0.45 (0.34)	-0.79 (0.41)	-0.49 (0.25)	--
High vol. OG*snow	0.91 (0.34)	--	0.35 (0.70)	--
Snow depth	-2.90 (0.90)	--	-2.65 (0.82)	--
*w*AIC	0.28	0.16	0.11	--
Second-growth vegetation models				
Young SG	0.62 (0.41)	-0.25 (0.47)	0.67 (0.38)	--
Young SG*snow	-0.25 (0.91)	--	-1.14 (0.73)	--
Old SG	-0.25 (0.41)	-0.66 (0.44)	--	--
Old SG*snow	0.66 (1.20)	--	--	--
Snow depth	-2.00 (1.11)	--	-1.60 (1.07)	--
*w*AIC	0.48	0.22	0.11	--

Table 5.3. Relative Effect Size of Covariates

Relative effect sizes (RE) of covariates in the top-ranked model for each covariate group.

Variable	***β (85% CI)***	***10% of range[a]***	***RE (85% CI)***
Forage covariates			
Total biomass	-0.02 (-0.08, 0.05)	0.68	0.99 (0.94, 1.04)
Total bio*snow	-0.16 (-0.30, -0.01)	0.18	0.96 (0.91, 1.02)
Snow depth	-1.27 (-2.58, 0.03)	0.18	0.80 (0.63, 1.01)
Landscape covariates			
Edge density	-0.01 (-0.02, -0.006)	2.54	0.96 (0.94, 0.98)
Edge*snow	0.03 (0.003, 0.051)	0.18	1.02 (1.00, 1.03)
Road density	-0.02 (-0.04, -0.01)	2.54	0.94 (0.91, 0.97)
Road*snow	0.02 (-0.01, 0.05)	0.18	1.01 (0.99, 1.02)
Southing	0.002 (0.000, 0.004)	17.00	1.04 (1.00, 1.08)
Southing*snow	0.007 (0.003, 0.011)	0.18	1.14 (1.06, 1.22)
Snow depth	-2.34 (-2.58, 0.03)	0.18	0.66 (0.55, 0.78)
Old-growth covariates			
Low volume OG	0.09 (-0.34, 0.52)	0.10	1.01 (0.97, 1.05)
Low volume*snow	0.004 (-0.84, 0.84)	0.18	1.001 (0.96, 1.05)
Med. volume OG	0.09 (-0.42, 0.61)	0.10	1.01 (0.96, 1.01)
Med. volume*snow	0.21 (-0.84, 1.26)	0.11	1.01 (0.97, 1.06)
High volume OG	-0.45 (-0.94, 0.05)	0.10	0.96 (0.91, 1.00)
High volume*snow	0.91 (-0.48, 2.29)	0.18	1.01 (0.99, 1.04)
Snow depth	-2.90 (-4.19, -1.60)	0.18	0.60 (0.48, 0.93)
Second-growth covariates			
Young SG	0.62 (0.04, 1.21)	0.10	1.06 (1.00, 1.13)
Young SG*snow	-0.25 (-1.56, 1.06)	0.18	0.99 (0.97, 1.01)
Old SG	-0.25 (-0.84, 0.35)	0.10	0.98 (0.92, 1.04)
Old SG*snow	0.66 (-1.07, 2.40)	0.18	1.02 (0.97, 1.06)
Snow depth	-2.00 (-3.60, -0.41)	0.18	0.70 (0.53, 0.93)

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CHAPTER 6. CONCLUSIONS

The research presented here contributes substantially to our understanding of ungulate ecology, and to the body of knowledge required to manage and conserve populations of Sitka black-tailed deer, their habitat, and their dependent predators in Alaska and northern coastal British Columbia. Using emerging technology and careful study design, I describe survival patterns and other vital rates, and use these results to identify key environmental drivers of deer population dynamics. I then develop models of spatial selection during reproduction and winter, two key periods in the annual life cycle of deer, and identify underlying forces shaping patterns of selection in deer in both summer and winter. Comparing these results with previous studies of deer habitat selection, I resolve long-standing conflicts expressed by those studies about habitat selection by deer during winter. The resulting insights into deer ecology can be used to inform land and wildlife management and conservation actions in the coastal temperate rainforest ecosystem of North America.

6.1. ROBUST SURVIVAL MODELS FOR FAWNS

Estimating survival rates during life history phases with strong effects of age on survival, such as for many neonatal animals, remains challenging. With respect to estimating survival of neonates, I employed a new technology, vaginal implant transmitters, that enabled me to locate birth sites and capture fawns within hours and sometimes minutes of birth. However, I needed to test the utility of that technology for Sitka black-tailed deer within northern temperate rainforest. I also captured neonates opportunistically without the assistance of VITs, a method used frequently during other studies of neonate deer in North America. That allowed me to compare survival data derived from both capture methods. When some neonatal animals die before being detected by researchers, left truncation is introduced into the data. This is problematic if the left-truncated animals missing from the sample had different values of covariates than those sampled, or different odds of daily survival (e.g., newborn animals are much more vulnerable than 2-day old animals, or if animals with low birth-weights die disproportionately). I demonstrate the potential biases that can be introduced into survival models by left truncation of data using

neonatal deer fawns, some captured at birth (i.e., untruncated data) and some captured within 10 days of birth (i.e., left-truncated data).

I found systematic negative biases of up to 31% in survival estimates from the left-truncated data, resulting from over-estimates of daily survival rates during the first 30 days of life. In addition, I found that left truncation of the data resulted in incorrect selection of top-ranked covariates in survival models, and incorrect estimates of covariate parameters including beta coefficient magnitude and direction. As a result, I conclude that ecological inference and estimates of survival rates from left-truncated data are likely to be biased. However, I suggest a practical solution, namely: 1) every effort be made to capture true neonates; 2) consistent capture methods, using at least in part non-truncating techniques, be implemented across years and study areas; and 3) exclusion of left-truncated data from survival estimates until age-dependent survival rates survival rates converge with those calculated from non- truncated data.

Our results are important for researchers modeling survival in organisms with strongly age-dependent survival patterns. This work was also critical for completion of subsequent analysis in this dissertation, I used only fawns captured at birth (i.e., untruncated data) for summer survival analysis in subsequent chapters, as daily survival rates between left-truncated and untruncated samples did not converge until 30 days of age. However, I did include left-truncated data in winter survival analysis, after this 30-day period was well past, thus increasing sample size and ability to make ecological inference regarding drivers of winter survival.

6.2. EFFECTS OF ENVIRONMENTAL VARIABILITY ON POPULATION DYNAMICS OF DEER

Previous studies of deer in Southeast Alaska and coastal British Columbia indicated winter weather and snow depth as the primary environmental drivers of deer population dynamics. Nonetheless, environmental drivers likely act differently on each segment of the population. I examined those effects on adult female deer and their neonate fawns by developing a matrix-based population model incorporating empirically derived models of age-specific rates of survival, and rates of pregnancy and fecundity. The underlying vital-rates models included both environmental covariates such as winter severity and timber harvest regime of resident watershed, as well as individual covariates such as mass, sex, and age. Best-fit models (based on

AIC ranking; Burnham & Anderson 2002) for each vital rate were then used to estimate mean vital rates, inter-annual variability, and process vs. sampling variance. I also estimated inter-annual process variance of the covariates themselves. The process variance of each vital rate and covariate was then used to perturb the population model, resulting in elasticities for vital rates and covariates based on their effect on perturbed population growth rate (λ) compared to the mean λ. I found that whereas prospective elasticity analysis of vital rates predicted that changes to adult survival would have the greatest influence on population dynamic, retrospective analysis revealed that fawn survival rates had the greatest influence on population growth rates based on observed levels of process variance. In addition, winter severity had the greatest effect of all covariates based on levels of process variance, followed by gender ratios of fawns. I conclude that inter-annual variability in Sitka black-tailed deer populations is likely most strongly affected by severity of winter weather, although factors that affect fawn sex ratios, such as buck to doe ratios (Mysterud et al. 2002), could also play an important role.

6.3. SPATIAL SELECTION BY REPRODUCTIVE DEER RELATIVE TO FORAGE AND PREDATION RISKS

Adult female deer varied patterns of selection by reproductive phase, as well as within reproductive phase. Deer responded strongly to predation risk from bears and wolves, as well as to forage biomass. During gestation, deer increasingly selected for forage, avoided bear predation risk, and tolerated wolf predation risk as parturition neared. After parturition, deer continued to strongly avoid bears, gradually increased avoidance of wolves, and gradually decreased selection of forage as fawns aged. If fawns died, deer greatly increased selection for forage then gradually relaxed forage selection, increased avoidance of wolves, and increasingly tolerated bears through time.

Among individuals, deer with more forage available to them also had less predation risk on average within their home ranges, indicating that home-range quality varied. Deer in high-quality home ranges relaxed selection for forage, and avoidance of predation risk, relative to those in poor-quality home ranges. Yet body condition was not correlated with home-range quality, and instead was correlated with positive selection for forage. A previous study (Brinkman et al. 2011) documented lower deer density in poor-quality habitats in the study area,

and differences in deer density by habitat quality is a likely explanation of my results. If deer density is higher in high-quality habitats, fitness benefits of those habitats decrease through resource competition (McLoughlin et al. 2006), and some deer may select instead for other, lower-quality habitats (McLoughlin et al. 2006; van Beest et al. 2014). However, some deer appear to do better than others regardless of home-range quality, indicating that individual heterogeneity may play an important role in determining fitness outcomes (Bock & Jones 2004; McLoughlin et al. 2007; Weladji et al. 2008), and ultimately population dynamics, for this species.

6.4. THE IMPORTANCE OF SNOW: PLASTIC SPATIAL SELECTION BY DEER IN WINTER LANDSCAPES

I sought to unify conflicting results from past studies of deer winter selection in Southeast Alaska by including daily snow depth maps as covariates of deer spatial selection. I found snow depth to be by far the most important covariate of deer spatial selection in winter. Snow depth also influenced direction and magnitude of selection towards vegetation classes and landscape covariates. Importantly, deer selection towards productive old-growth forest types increased substantially with increasing snow depth, whereas selection towards young second-growth forest types declined and selection for old second growth increased. At low snow depths, deer selected slightly for medium-volume old growth and strongly for young second growth, likely because of abundant forage within these forest types, and avoided high-volume old growth and old second growth. In addition, deer selected strongly for south facing slopes and avoided habitat edges and roads at low snow depths, and increased the strength of selection for these features as snow depth increased. These results resolve much of the dissonance between past studies, in which studies on northern, deep-snow islands found strong selection for productive old-growth forests (Schoen & Kirchhoff 1985), whereas other studies on southerly islands found weakly positive or even negative selection for old growth, and positive selection for young second growth (Doerr et al. 2005; Yeo and Peek 1992). These results were also in agreement with Person et al. (2009), who found strong effects of elevation, canopy cover, slope, and aspect on deer selection. These landscape covariates are the linear components that best predict snow depth in Southeast Alaska

(Hanley et al. 2012), indicating that snow depth, while not systematically measured through time and space, was likely the primary driver of deer selection.

There was considerable variability in selection among individuals, some of which was explained by functional responses to availability of vegetation classes. Availability of young second growth to deer did not influence strength of selection, but deer were significantly more likely to select for old second growth when it was more available to them. Selection for old second growth declined significantly when alternatives, namely productive old-growth forest types, were available to them. This indicated that deer selection is plastic, with deer using old second growth for movement when it is widely available and old growth with adequate canopy to intercept snow is not available. However, old second growth does not have adequate forage to support deer through the winter, and young second growth is avoided during deep snow, making preservation of productive old growth as insurance during deep-snow winters a critical component for deer management.

6.5. FUTURE DIRECTIONS AND NEEDS

This dissertation addresses a number of important, unresolved questions regarding the population ecology of Sitka black-tailed deer, and of ungulates in temperate ecosystems more broadly. However, there are many outstanding questions that remain for deer in Alaska, some of which can be answered with data I obtained but have not yet analyzed, and some of which will require further field work to collect the relevant data. Important questions that can be addressed using my existing data include: a) do deer select habitat during winter at different scales (i.e., annual home ranges within watersheds, core winter areas within home ranges, and patches/movements within core winter areas), and how forage depletion through time during winter may affect selection patterns (van Beest et al. 2010); b) do deer develop patterns of resource selection from birth independently or are their movements and selection strongly correlated with their mothers; c) what are the fitness consequences for adult females and their offspring of the patterns of resource selection I document here; and d) do deer select patches of second growth that are pre-commercially thinned, a widespread forestry practice purported to benefit deer through increased forage production in old second-growth habitats but the realized value of which to deer is unknown.

Questions of primary importance, but which require further data collection to answer include: e) empirical testing of wildlife use (including deer) of various designs of restoration clearings in old second-growth, which are currently being implemented but not monitored for efficacy to wildlife; and f) real-time effects of timber harvest on deer, in which a before-after control-impact design is implemented before a timber sale and effects on radio-collared deer, forage, and potentially predators are monitored.

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